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CONTENTS

PAGE

SOUTHWOOD, T. R. E., Ph.D., A.R.C.S., F.R.E.S. The structure of the eggs of the Terrestrial Heteroptera and its relationship to the classification of the group . . . . . 163–221, 13 figs.

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THE STRUCTURE OF THE EGGS OF THE TERRESTRIAL HETEROPTERA AND ITS RELATIONSHIP TO THE CLASSIFICATION OF THE GROUP.

By T. R. E. Southwood, Ph.D., A.R.C.S., F.R.E.S.[1]

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With 13 Text-figures.

Introduction 163
Methods 164

THE EGGS OF THE TERRESTRIAL HETEROPTERA

Structure 165
Oviposition 175
Development 177
Hatching 178

A SYSTEMATIC CONSIDERATION OF THE EGGS OF THE FAMILIES OF THE GEOCORISAE

Pentatomomorpha
Pentatomoidea 181
Coreoidea 188
Lygaeoidea 191
Pyrrhocoroidea 195
Aradoidea 195

Cimicomorpha
Reduvioidea 198
Tingoidea 201
Cimicoidea 202

Geocorisae incertae sedis 206

Summary 207
Acknowledgments 207
References 208

Introduction.

The eggs of the Heteroptera have always been noted by biologists for their remarkable diversity of form. Besides being described by the field naturalist (e.g. Kirby and Spence, 1826), their structure has been investigated in detail by microscopists (e.g. Leuckart, 1855).

[1] Now at Imperial College Field Station, Silwood Park, Sunninghill, Berks.

Reuter (1910) stressed the value of egg structure in classification, but he was strongly attacked by Ekblom (1929), who said: "Even the eggs have been taken as a basis for classification. . . . As I have shown in my previous papers, the shape of the egg is closely connected with the method of egg-laying and the structure of the ovipositor. Moreover the shape varies considerably even within the same group".

Ekblom's objection to the actual shape of the egg is partially justified, for this, like the posture of the egg when laid (Michalk, 1935) is variable within a family. These characters are superficial, but the structure of the micropylar apparatus and the method of hatching (i.e. structure of egg-burster and presence or absence of an operculum) do not vary within recognised groups, even when the method of egg-laying and the structure of the ovipositor does. For example, the ovipositor of the Lygaeidae is well developed with elongate pointed valvulae, whilst that of the Largidae is much smaller and the valvulae are flap-like; yet the egg structure in these two related families is similar. Another example is in the Aradoid families Meziridae and Aneuridae; the ovipositor of *Aneurus* is greatly reduced and yet the eggs of both families are similar. Leston (1954*b*) has described the extremely elongate and very atypical ovipositor in a Pentatomid, *Birketsmithia anomala* Leston, but he states that ovarian eggs, although elongate, were of the typical Pentatomid form.

Leston, Pendergrast and Southwood (1954) proposed that two main groups should be recognised within the Geocorisae (*sensu* Dufour, 1833); these were the Pentatomomorpha and Cimicomorpha. They are distinguished by differences in their trichobothria, spermathecae, wing venation, male genitalia, salivary glands and egg structure. The evidence from the trichobothria was based on the work of Tullgren (1918), from the male genitalia partly on the work of Pruthi (1925). Southwood (1955*b*) has already given an account of the distinguishing features in the salivary glands and the present paper shows in detail how the egg structure supports the division into Pentatomomorpha and Cimicomorpha.

Methods.

The present studies are based on the examination of living eggs, eggs preserved in alcohol or Bouin's fluid, ovarian eggs and empty egg-shells. Their structure was elucidated by three main methods:

(*i*) *Whole mounts—either of the complete egg or the egg-shell.* Living eggs were fixed in Bouin's or Carnoy's fluids and cleared in xylol-phenol. Occasionally they were stained in acid fuschin or basic fuschin, with the latter followed by concentrated sodium chloride solution. Xylol was used as the clearing agent after staining and also for egg-shells. The material was mounted in canada balsam or occasionally in napthrax.

(*ii*) *Sections.* Beament (1947) showed that, if previously fixed in picric acid, egg-shells could be softened by soaking in dilute potassium hydroxide solution for ten minutes or so without causing any structural alteration. Eggs were treated in this manner, then washed in water and, after passing through 70 per cent., 95 per cent. and absolute alcohol, placed in methyl benzoate with 1 per cent. celloidin for 12 hours. They were then transferred to benzene for 15 minutes, followed by wax and benzene and, lastly, into molten wax (m.p. 60° C.) in which they were embedded prior to sectioning with a micro-

tome. The sections were stuck on slides, dewaxed and mounted with canada balsam in the usual manner.

(*iii*) *Cobalt sulphide injection technique.* This method was devised by Wigglesworth (1950) for insect tracheoles and was used by Wigglesworth and Beament (1950) for the investigation of the respiratory mechanisms of the eggs of various insects. The apparatus and method is described in detail by Wigglesworth (1950). It consists in principle of evacuating the air from the spaces in the egg and then submerging it in a solution of cobalt naphthenate in petroleum, so that all these spaces become filled with this solution. The egg is then subjected to hydrogen sulphide and black cobalt sulphide is precipitated in all the spaces previously filled with air.

Living eggs were treated in this way to examine their respiratory mechanisms; sometimes very late ovarian eggs were treated and then the true micropyles, which become occluded by cement after laying, became filled with the black precipitate as well.

THE EGGS OF THE TERRESTRIAL HETEROPTERA.

Structure.

The formation of the chorion (egg-shell).

The ovaries of all Heteroptera are of the telotrophic type and, after the oocytes have accumulated yolk to their full size, they become surrounded by follicle cells and these secrete the chorion. Gross (1901, 1903) studied the formation of the chorion in various Pentatomids, *Coreus*, *Pyrrhocoris*, and in two Mirids, Köhler (1903, 1907) in *Pyrrhocoris apterus* L, and Beament (1946*a*, 1947) in *Rhodnius prolixus* Stål. The latter describes the different form of the follicle cells at each stage of secretion of the chorion and also the detailed changes in the follicle cells of the micropylor region during its formation.

The follicle cells have been found to be binucleate by these authors and Beament (1946*a*) found that in transverse section each cell was divided by a median transecting bar and one nucleus was on each side of this bar. It has been found in *Anoplocnemus*, *Dysdercus* and *Rhinocoris* that the follicle cells are binucleate and in transverse section (fig. 1A) show the transecting bar similar to that found by Beament. The transecting bar stains with both Ehrlich's haematoxylin and basic fuschin in the same way as the cell boundaries.

In *Dysdercus* (fig. 1B) and *Anoplocnemus* the follicle cells are all similar in shape and size, except for slight flattening at the poles; this can probably be correlated with the similarity of all regions of the chorion. Gross (1901) found the same condition in various Pentatomids, with only modifications in the few cells that secrete the micropylar processes.

During the early stages of their development the egg cells of *Rhinocoris* are almost spherical in shape (fig. 1C), and the surrounding follicle cells are elongate. Towards the end of the yolk formation the eggs become more lengthened and the follicle cells, apart from those at the anterior poles, which will subsequently be the region of the operculum, become flatter (fig. 1C). During the later phases of chorion formation the follicle cells of the opercular region become extremely elongate (fig. 2A).

Beament (1946*a*, 1947) found in the egg of *Rhodnius*, which has much shallower follicular pits on the operculum, that the follicle cells at the anterior pole of the oocyte are only slightly longer than those surrounding the remainder of the egg. The follicle cells of the future opercular region have also been found by Gross (1903) to be extremely elongate in *Leptopterna dolabrata* L. and *Capsodes gothicus* Fallén.

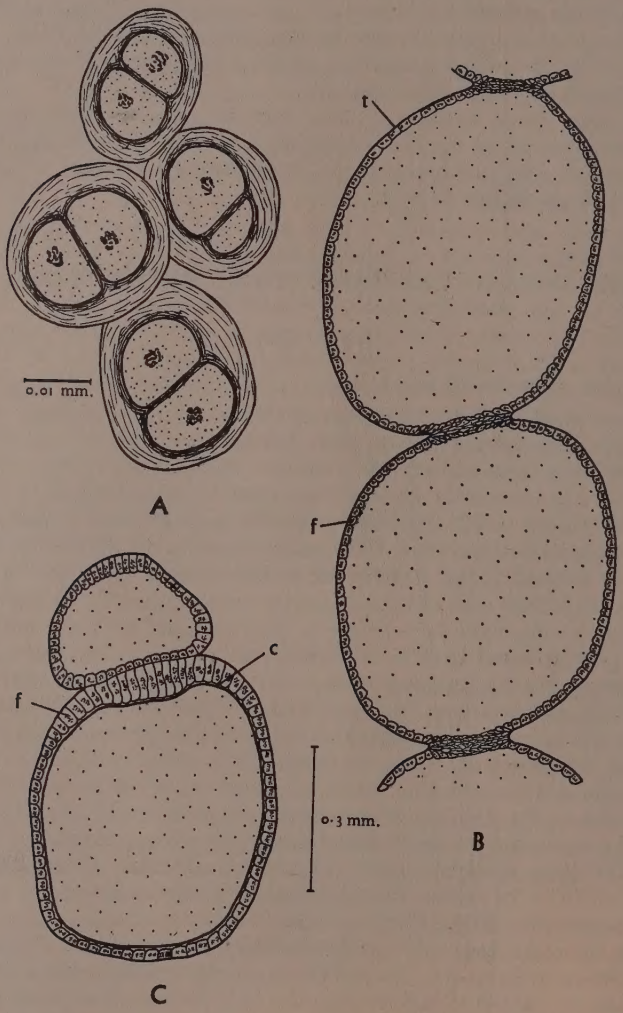
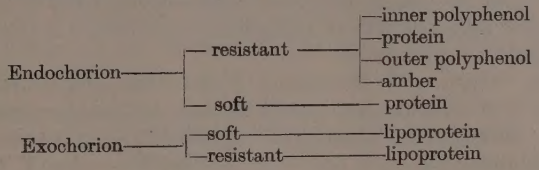


FIG. 1.—(A) *Rhinocoris*, T.S. of binucleate follicle cells just prior to the secretion of the chorion. (B) *Dysdercus*, L.S. ovaries during endochorion formation. (C) *Rhinocoris*, L.S. ovaries during endochorion formation. *c*, endochorion; *f*, follicle cells; *t*, tunica propria.

Chorion.

Beament (1946*a*) defined this as "that part of the egg lying outside the oocyte cell membrane, which is secreted by the follicle". He showed that in *Rhodnius* it consists of various layers :—



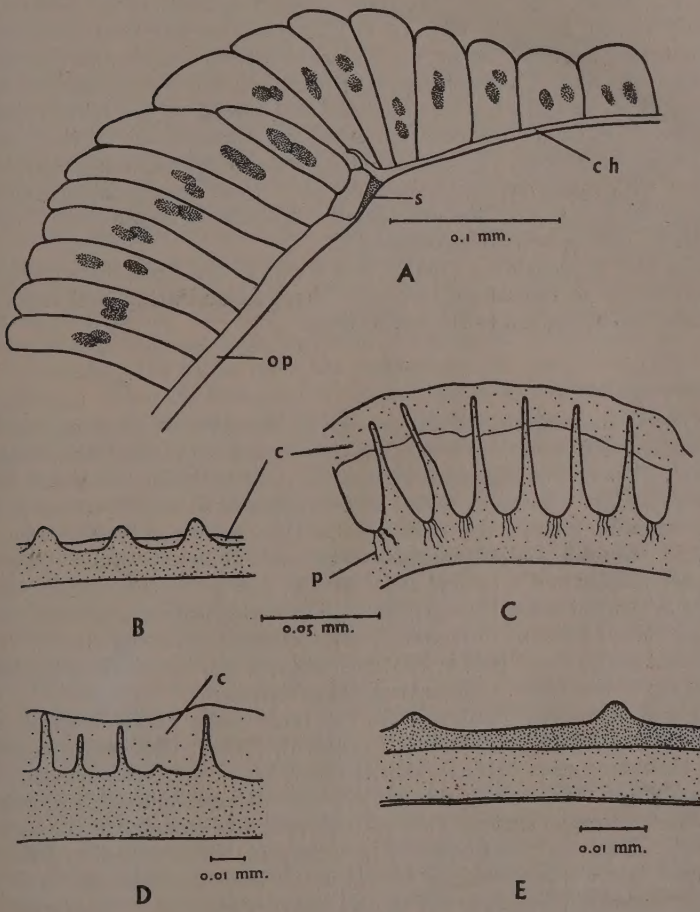


FIG. 2.—(A) *Rhinocoris*, L.S. through follicles in region of micropylar complex. (B–E) Sections through the chorion : (B) Ventral region of *Coptosoma*. (C) Ditto, dorsal region. (D) *Dalpada oculata* F. (E) *Myrmus miriformis* Fall. *c*, cement ; *ch*, extra-opercular chorion ; *op*, opercular chorion ; *p*, pore canals ; *s*, sealing bar.

Beament (1946*a*) found that during the secretion of the soft endochorion and the exochorion more material is laid down round the margins of the follicle cells, causing an hexagonal sculpturation.

The actual form of the chorion varies greatly within the suborder. This modification is, however, usually entirely a matter of the depth of the follicular pits; with shallow follicular pits an hexagonal sculpturation is produced, with deeper pits a punctate appearance.

In *Coptosoma cribrarium* F. the chorion of the dorsal and lateral regions of the egg has very deep follicular pits and at the base of these the pore canals are visible (fig. 2C); however, the chorion of the ventral region is thinner and the follicular pits are much shallower (fig. 2B). In *Dalpada oculata* F. (fig. 2D) the chorion is covered with small processes which represent, in all probability, irregularly formed follicular pits. A similar condition has been described in other Pentatomoids, but in many, e.g. *Nezara viridula* L. and *Zicrona caerulea* L. the chorion is smooth. The most complex pattern is found in *Eurydema pulchrum* Westwood (figs. 8D and E), where it seems that certain of the follicle pits get covered over, i.e. the follicle cells concerned get squeezed out by their neighbours and cease to secrete. The surface of the chorion of *Myrmus miriformis* Fallén is covered with numerous projections (fig. 2E); these are almost entirely due to differential secretion of the exochorion. A similarly rugose chorion occurs in the Mirid, *Strongylocoris leucocephalus* L.

Abalos and Wygodzinsky (1951) have found in the Triatominae that the form of chorionic sculpturation is a specific character and within that subfamily varies from the hexagonal to the rugose type.

Micropylar apparatus.

The classic investigation of the micropylar structure of insect eggs is that of Leuckart (1855), who considered that these canals served for the passage of the sperm. Gross (1901) disputed this, stating that their function was to allow gaseous exchange. Beament (1947) and Wigglesworth and Beament (1950) have investigated the so-called micropyles in three species of Heteroptera. In *Oncopeltus fasciatus* Dallas, Wigglesworth and Beament found that the micropylar process had a central canal for the passage of the sperm; this is occluded by cement when the egg is laid. The rest of the process has a porous structure which serves for the respiratory interchange of the egg.

Beament (1947) found that in *Rhodnius prolixus* Stål the canals in the rim of the shell are of two types. These he distinguishes as:

(*a*) *Pseudomicropyles*[1] that end in the inner layer of the chorion (the "resistant endochorion protein layer" Beament, 1946*a*); they may or may not open on the outer surface of the chorion and are filled with a porous material. The function of these, the Leuckart's canals of many authors, is entirely respiratory.

(*b*) *True micropyles* that are open at both ends, but occluded in the laid egg by cement. Their course is frequently irregular and it is considered by Beament (1947) that they are produced by follicle cells which have been squeezed out of the pseudomicropylar ring in the earliest stages of secretion. It is considered that it is by these that the sperms enter the eggs. Wigglesworth and Beament

[1] Since the completion of the manuscript Dr. H. E. Hinton (1955, *Proc. R. ent. Soc. Lond.* (A) **30**: 1–14) has suggested the term, aeropyle, for these canals.

found only pseudomicropyles in *Cimex lectularis* L. and, as they pointed out, it seems probable that true micropyles do not exist, for Cragg (1920, 1923) and Abraham (1934) have shown that the egg is fertilised in the ovary.

In the course of the present study it has been found that there are, in fact, two distinct types of micropylar apparatus in the terrestrial Heteroptera. These correspond to those first discovered by Leuckart (1855) and they form one of the characters for the division of the group into Pentatomomorpha and Cimicomorpha. They are:

(i) Micropylar processes (Pentatomomorpha).
(ii) Pseudomicropyles and micropyles (Cimicomorpha).

(i) *Micropylar process.* A structure, normally raised above the surface of the chorion, consisting of a "central canal" (for sperm passage) surrounded by porous protein, the "air-sponge" (which allows gaseous exchange).

In *Oncopeltus fasciatus* the micropylar process (fig. 3A) is raised above the surface of the chorion as a club-like structure; the apical region forms the "cup" with the "aperture" leading to the canal. The cup narrows to form the "stem" and at its base the exochorion of the micropylar process becomes continuous with that of the chorion. The canal, which serves for the passage of sperm, narrows considerably behind the aperture and runs down the centre of the stem and into the chorion, which is thicker at the base of the micropylar process than elsewhere. The canal then turns sharply at right angles and runs in the lower part of the chorion for some distance as the "transverse canal", eventually terminating in a pore opening on the inside of the chorion. The transverse canal, which has not previously been noted, is very thin and irregular in its course and length.

Surrounding the canal, from the aperture to the transverse region, is the air-sponge. When the living egg is injected with cobalt sulphide the air-sponge becomes grey in the cup and black in the stem regions; at its base it is continuous with the resistant endochorion layer of the chorion. As was stated by Wigglesworth and Beament (1950), this shows that the air-sponge serves for the gaseous exchange of the egg. When heated with 2 per cent. triketohydrinidine-hydrate in glycerine the air-sponge becomes blue in colour, showing that it is predominantly protein in nature and probably similar to the resistant protein layer of the endochorion described in *Rhodnius* by Beament (1946*a*).

Micropylar processes essentially similar to the above occur throughout the Pentatomomorpha and vary in number from two to some hundreds per egg. A common variation is for the stem to be absent as in *Aneurus laevis* F. (fig. 12F), *Piesma quadrata* Fieber (fig. 11L), *Dysdercus fasciatus* Signoret (fig. 11J), and *Sehirus bicolor* L. (fig. 7D). In all these species a transverse canal has been found and the length of this canal often varies from one process to another, as is particularly well seen in *S. bicolor* (fig. 7B).

In the Pentatomidae the cup region is but slightly differentiated from the stem. The latter is especially long in the Amyoteinae, e.g. *Zicrona caerulea* (fig. 8K). In this species the transverse canal appears to be absent and the micropylar canal projects slightly into the cavity of the egg-shell. In *Chrysocoris* and other Scutellerinae, the micropylar processes are very small, forming merely protruberances in which the aperture is situated; but by contrast with *Zicrona* the transverse canal is present.

The most complex micropylar processes were found in the Brachyplatidae. In

Brachyplatys the cup is almost spherical with a slight median constriction in surface view (fig. 9J). It consists of a clear outer region which, although staining slightly with basic fuschin, remains absolutely clear when injected with cobalt sulphide; it would appear that this region is hollow (fig. 9K). Placed

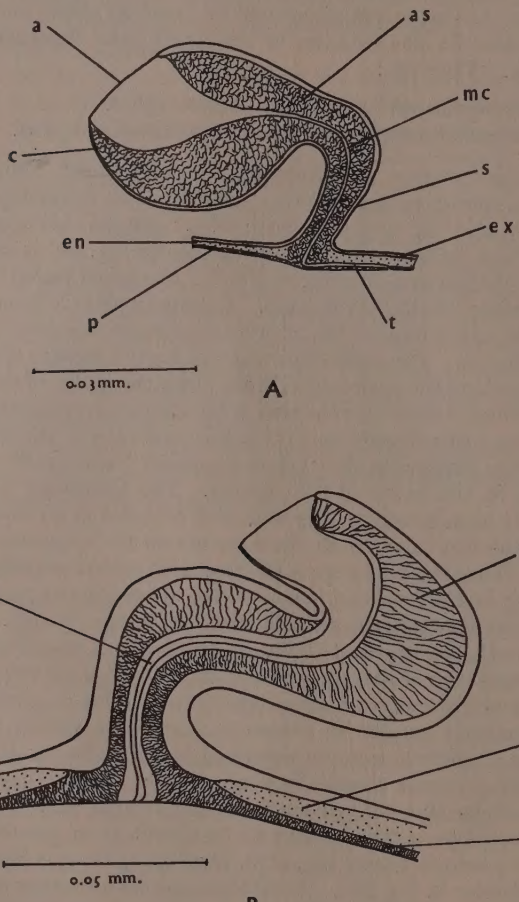


FIG. 3.—L.S. of micropylar processes. (A) *Oncopeltus fasciatus* Dallas. (B) *Myrmus miriformis* Fall. *a*, aperture; *as*, airsponge; *c*, cup; *en*, endochorion; *ex*, exochorion; *mc*, micropylar canal; *p*, porous protein layer of endochorion; *s*, stem; *t*, transverse region of micropylar canal.

centrally, but towards the base of the cup and surrounded by this hollow region, is the air-sponge; this communicates to the exterior dorsally by a narrow funnel-like passage. This passage, surprisingly, becomes only light grey when injected with cobalt sulphide; running through its centre and through the air-

sponge is the micropylar canal. As in the Amyoteinae, this appears to lack a transverse region and projects slightly into the cavity of the egg-shell. It can be seen in side view that the funnel-like passage and the canal are slightly curved (fig. 9L). In *Coptosoma cribrarium* the structure of the process is even more complex, with the micropylar canal projecting from the top, (i.e. out of the aperture).

The paired S-shaped micropylar processes of the Rhopalidae have been discussed by many authors, e.g. Butler (1923), Poisson (1933); the latter was of the opinion that one of the processes (that on the pseudoperculum) was purely respiratory and lacked a micropylar canal. Both processes are, however, similar in structure and sections have shown this clearly (fig. 10N). The micropylar canal has remarkably thick walls. The fusion of the air-sponge with the resistant protein layer of the chorion is clearly seen, as is the break in the soft endochorion layer just below the micropylar process. The transverse region of the canal appears to be absent.

Micropylar processes are numerous in many of the Coreidae (*sensu stricto*). However, they are often very small, consisting as in *Cletus trigonus* Thunb. (fig. 10E), of protruberances on the chorion below which a cylinder of air-sponge surrounds the micropylar canal.

(ii) *Pseudomicropyles and micropyles.* Canals running in the rim of the chorion, the former serving for gaseous interchange and the latter for sperm passage.

The most complete form of this type of apparatus is found in some Reduviids, which are probably the most primitive of the Cimicomorpha.

In *Rhinocoris* sp. the rim of the chorion ends in a reticulum, the network region, the extreme apex of which is joined to the top of the operculum (fig. 4A) by a thin scolloped veil. The network region consists of a mesh of " canals "; at the base of this region, above the spermatic groove, these network canals run into the pseudomicropyles (fig. 4C). The pseudomicropyles, with the true micropyles, mark the " micropylar region ", which is between the spermatic groove and just below the level where the operculum is joined to the wall of the chorion by the sealing bar.

When the egg is injected with cobalt sulphide the network canals and the pseudomicropyles become grey or black; this shows that they are part of the gaseous exchange system of the egg and also enables their structure to be further elucidated. The pseudomicropyles end in the resistant protein layer of the endochorion as small bulbous cavities; above the sealing bar they usually expand to form another cavity and they frequently do so again just below the network. From the lowest horizontal canal of the network a short canal often arises; this terminates in a pore. When injected with cobalt sulphide the centres of these pores remain clear, but their margins become grey. This is interpreted as being due to the cobalt naphthenate washing out of the aperture of the pore.

The true micropyles occur occasionally round the rim of the chorion; they do not appear grey or black after injection with cobalt sulphide, as they are blocked with cement after laying, but in ovarian eggs thus injected they become filled with precipitate. True micropyles run from the lower margin of the spermatic groove, where they have a funnel-like opening, towards the posterior pole of the egg until the level of the sealing bar. There they become very fine

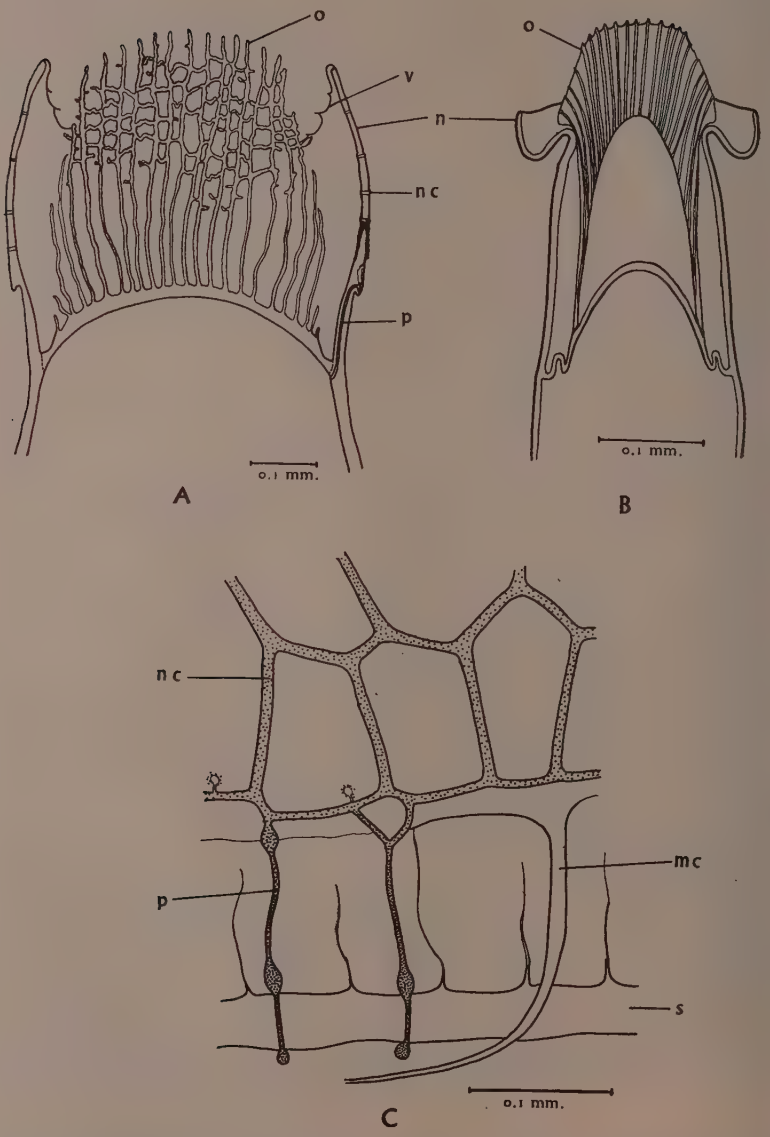


Fig. 4.—(A) *Rhinocoris*, L.S. operculum and micropylar regions. (B) *Nabis flavomarginatus* Scholtz, ditto. (C) *Rhinocoris*, surface view of base of micropylar region after cobalt sulphide injection. *mc*, true micropyle ; *n*, network region ; *nc*, network canal ; *o*, operculum ; *p*, pseudomicropyle, *s*, spermatic groove ; *v*, veil.

and turn almost at right angles, following an irregular course and terminating as a fine opening on the inside of the chorion.

Beament (1947) has described the arrangement in *Rhodnius*, where the network region is absent and the micropylar region reduced. It is only in the Reduviidae that pseudomicropyles and true micropyles have both been found.

In the Cimicoidea true micropyles are absent and in the Cimicidae and Anthocoridae this is certainly correlated with their fertilisation before ovulation and before the formation of the chorion. Carayon (1954 and *in litt.*) has found that in the Tingidae, Nabidae, Microphysidae, Miridae, Isometopidae and Joppeicidae fertilisation does not occur until after ovulation. If the interpretations of the present author are correct and true micropyles are absent in the eggs of the Nabidae, Microphysidae and Miridae, then their fertilisation is an unsolved problem. It may be that further work will show that one or two of the structures considered here as pseudomicropyles are, in fact, open at both ends.

In the Nabidae, e.g. *Nabis flavomarginatus* Schultz. (fig. 4B), the network region is reduced, but still present. The pseudomicropyles are very long. The most highly evolved Cimicoidea, the Miridae, have completely lost the network region. Their eggs are laterally compressed, hence the opercula are somewhat elliptical in shape. The pseudomicropyles tend to be concentrated, perhaps as a result of the asymmetry, at the narrow sides of the rim of the chorion, as in *Leptopterna dolabrata* (fig. 13G). The extreme condition is reached in eggs, like those of *Dicyphus stachydis* Reuter (fig. 13F), in which the pseudomicropyles are present only at the corners, where the rim of the chorion is produced to form a process. These processes differ from true micropylar processes in lacking the porous protein air-sponge and their canal is pseudomicropylar, not micropylar.

Pseudomicropyles have not been found in the Tingidae, although the eggs of *Tingis ampliata* H.-S., *Dictyonota strichnocera* Fieb. and *Stephanitis rhododendri* Horvath have been examined and the latter injected with cobalt sulphide. Furthermore, other workers have not described any structures that could be considered as pseudomicropyles (see p. 201). The network is, however, always present; in *Telonemia scrupulosa* Stål it is large and directed upwards covering the operculum, as described by Roonwal (1952). In *Tingis ampliata*, *Dictyonota strichnocera* and *Stephanitis rhododendri*, however, it is smaller, reflexed back and covered with the operculum.

True micropyles, distinguished because they are open at both ends and always, it seems, more or less irregular in their course, have been found in *Stephanitis rhododendri* by Johnson (1936) and the author (fig. 13B) and in *Teleonemia scrupulosa* by Roonwal (1952). It is most noteworthy that, unlike the true micropyles of the Reduviidae, these open on to the inner surface of the rim of the chorion. However, in those species with a reflexed rim, e.g. *Stephanitis rhododendri*, this subsequently becomes the outer surface.

Opercular apparatus or egg-cap.

Beament (1946*a*) described the operculum of *Rhodnius*. A similar operculum is present in all the Cimicomorpha and it may be defined:

(1) Separated from the rest of the chorion by a distinct sealing bar.

(2) Differing from the rest of chorion in structure, usually with much deeper follicular pits and with thicker amber and soft endochorion layers.

(3) Surrounded by the micropylar apparatus, which is situated in the rim of the chorion.

The operculum is very thick in some Reduvids and Nabids, e.g. *Rhinocoris* (fig. 4A) and *Nabis flavomarginatus* (fig. 4B), where the follicular pits are very deep and the thick amber and soft endochorion layers can be plainly seen. When injected with cobalt sulphide these follicular pits become filled with black precipitate and they undoubtedly play some part in the gaseous exchanges of the egg. In *Rhinocoris* the rim of the chorion is joined to the top of the operculum so that a sealed air space is present between the operculum and the rim of the chorion, whilst the follicular pits of the operculum have partial or complete transverse portions (fig. 4A).

Again, in *Nabis flavomarginatus* the space between the rim of the chorion and the operculum appears to be sealed, as it remains colourless after injection with cobalt sulphide, as does the large space between the bases of the follicular pits and the endochorion of the operculum. The follicular pits themselves are completely open and become completely black when treated with cobalt naphthenate as above.

The operculum of the Miridae is laterally compressed ; this is especially so in *Leptopterna dolabrata* (fig. 13G), where it is completely covered by the rim of the chorion. In this species the deep follicular pits become black after injection with cobalt sulphide.

The actual shape of the operculum of the Miridae has many different forms and some of these have been figured by Kullenberg (1946). In *Lygus pratensis* L. the operculum is thin and the follicular pits almost non-existent, whilst in *Miris striatus* L. the central pits are shallow and those at the margins are deep, and in *Orthocephalus mutabilis* Fallén all the opercular pits are deep.

In the Anthocoridae, Cimicidae, Microphysidae and Tingidae the follicular pits of the operculum are generally shallow, but Sands (1954) has described what would appear to be a thick operculum in *Acompocoris pygmaeus* Fallén (Anthocoridae).

The true operculum of the Cimicomorpha, with the weak point in the sealing bar, aids in the eclosion of the larva and its presence is correlated with the absence of the median egg-burster in this group (see p. 178). As the investigations with the cobalt sulphide injection technique have shown, it may also play some part in the respiratory interchange of the egg.

A so-called operculum is present in various Pentatomomorpha (e.g. Pentatomidae, Brachyplatidae), some Coreidae and Rhopalidae. It is proposed to refer to this structure as the " pseudoperculum " because it differs from the true operculum of the Cimicomorpha in :

(1) Lacking a distinct sealing bar.

(2) Having the same structure as the rest of the chorion.

(3) Not bearing any fixed relationship to the micropylar apparatus; this may surround it or occur both on and off it.

In functional contradistinction to the true operculum, the pseudoperculum plays no part in the gaseous interchange of the egg. It consists of a line of structural weakness, often no thinner than the rest of the chorion, that facilitates eclosion and it is noteworthy that a pseudoperculum is present only in those eggs with thick chorions. The differing forms of the pseudopercula and the variation in their relationship to the orientation of the embryo and the

position of the micropylar processes suggest that they have been evolved several times in the Pentatomomorpha.

In *Coptosoma cribrarium* the pseudoperculum shows greater differentiation from the remaider of the chorion (fig. 9F) than in any other Pentatomomorpha ; in general the condition is similar to that in *Anoplocnemus phasiana* F. (fig. 10G).

In some Pentatomids a pseudoperculum appears to be present as a circle inside the ring of micropylar processes and it is often shown by authors as a distinct line. On eclosion, however, the chorion splits more or less irregularly, as is seen in *Dalpada oculata* (fig. 7G) and *Chrysocoris* sp. (fig. 8A). However, in most Pentatominae and Amyoteinae the pseudoperculum is, in fact, present as a circle inside the micropylar processes and is forced up at eclosion. In some Dinodorinae (*Megymenum*) (Miller 1934), where the eggs are laid on their sides and closely adpressed pole to pole, the pseudoperculum occurs on the upper surface. A similar method of oviposition in certain Coreidae, e.g. *Anoplocnemus phasiana* (fig. 10H), is associated with a similar lateral pseudoperculum.

In the Rhopalidae, e.g. *Chlorosoma schillingi* Schu. (fig. 6D), a pseudoperculum is present on the dorsal surface near the cephalic pole, separated from the rest of the chorion by a slightly thinner (fig. 10N) and paler ring.

Jordan (1933) has described and figured what is probably a pseudoperculum in *Kleidocerys resedae* Panzer (Lygaeidae). As in some Pentatomids, the margins of the egg-cap do not correspond with the line of fracture at eclosion.

Oviposition.

Michalk (1935) classified the eggs of the Heteroptera on their oviposition site in ten categories. These divisions—criticised first by Leston (1953*a*)—are much too fine and cut right across family barriers and are artificial from the ecological aspect. Oviposition sites can, however, be satisfactorily grouped into four loose categories based on their relationship to the environment :

(1) Exposed, e.g. on leaves of plants, as in Pentatomidae, Coreidae, Piesmidae, Neididae, some Lygaeidae (e.g. *Nysius*), some Reduviidae (e.g. *Sycanus*).

(2) Semi-exposed, e.g. in the soil, under rocks, amongst fallen leaves, in the axils of stems, as in some Cydnidae, most Lygaeidae, Pyrrhocoridae, most Reduviidae, some Miridae (e.g. *Strongylocoris*).

(3) Embedded in plant tissue that is either dead or becomes so before the eggs hatch, as in Nabidae and some Miridae.

(4) Embedded in or intimately associated with living plant tissue, as in Tingidae, Anthocoridae and some Miridae.

Eggs in group (1) must be quite self-sufficient in their water supply, as has been shown with *Myrmus miriformis* by Woodward (1952) ; they will frequently be liable to exposure to direct sunlight and it is amongst such eggs that the thickest and frequently dark chorions are found, e.g. *Coptosoma cribrarium* 60μ and *Anoplocnemus phasina* 25μ. Eggs laid in this manner are also often copiously covered with cement so as to form an ootheca (see later p. 176) and their micropylar processes are frequently long and few in number.

Eggs in group (2) are usually in a semi-humid or humid atmosphere and thus

are not subject to such extremes of physical environment as those that are fully exposed. Their chorion is normally thin and unpigmented, e.g. *Sehirus bicolor* L. 2μ, and their micropylar processes are short and numerous.

The eggs in group (3) are typified by those of *Nabis limbatus* Dahlb. and *Leptopterna dolabrata*. These eggs are laid in the autumn into the centres of the hollow stems of grasses, which may be living at the time so that water absorption can occur. The stems subsequently die and, according to their situation and subsequent fate, they may remain moist or become fairly dry, so that the conditions resemble those in group (2).

Eggs in or associated with plant tissue, group (4), are not liable to drying out and frequently absorb water, e.g. *Notostira erratica* L. (Johnson 1934*b*, 1937). It would seem probable that the major mechanical risks to be overcome in this type of oviposition are being crushed by the plant tissue or being overgrown by the surrounding bark.

Cement. During oviposition the eggs are covered with a cement secreted by various accessory glands of the female genitalia or by the intestine. Beament (1948) found in *Rhodnius* that although this cement, a tanned protein, covered the openings of the micropyles, those of the pseudomicropyles, which are somewhat higher, are always left free.

In many eggs laid in exposed situations the cement forms a more or less complete covering. In *Coptosoma cribrarium* the cement covers the whole of the outside of the chorion leaving air pockets at the bases of the follicular pits (fig. 2c). This is probably a poorly developed form of the ootheca of *Plataspis flavosparsa* Mont., described by Carayon (1949*a*), who found that it was secreted by certain specialised cells of the intestine.

The egg of *Zicrona caerulea* appears to be black, but this is due to complete covering (except for the tips of the micropylar processes) by a cement which becomes dark after secretion. On the pseudoperculum there are radial ridges leading in from each micropylar process towards the pole ; these are ridges of cement marking the positions in which the micropylar processes were temporarily stuck down to the pseudoperculum immediately after laying. The gradual erection of these processes has been described in great detail for *Picromerus bidens* L. by Mayne and Breny (1942).

Miller (1931, 1934) has described how certain Coreid eggs are covered with a " wax-like powder ". The author has found with *Anoplocnemus phasiana* that this is a wax that is only very slightly soluble in cold chloroform but much more readily dissolved in hot chloroform. In this property it closely resembles the wax on the chorion of the egg of the Fruit Tree Red Spider Mite (*Metatetranychus ulmi* Koch) described by Beament (1951).

Symbionts. The mechanisms for the transmission of the symbionts of insects have been reviewed by Carayon (1952). In *Rhodnius* the young larvae live in the same environment as the adults and become infected by *Actinomyces* that have passed out with the latter's excreta (Brecher and Wigglesworth, 1944). In the Pentatomidae, probably the Coreoidea, Neididae and a few Lygaeidae a secretion from the intestine containing symbionts is deposited on the outside of the eggs. The young larvae become contaminated by feeding on this after eclosion.

In Brachyplatidae (Schneider, 1940 ; Carayon, 1949*a*) pellets of symbionts are placed between the two rows of eggs (fig. 9c).

The Acanthosomidae differ from other Pentatomoidea in that the bacterial crypts lose connection with the digestive tract in the adult (Rozenkranz, 1939), but the eggs are infected by a special organ on the female genitalia that consists of many fine tubes filled with symbionts. In *Ischnodemus sabuleti* Fallén (Schneider, 1940) and *Cimex lectularius* L. (Buchner, 1923) the infection occurs in the earliest stages of development of the oocyte; in *Nysius* (Schneider, 1940) the mycetome is adpressed to the ovaries and a localised infection occurs.

Development.

During embryonic development various membranes are present and the following review is mostly based on the works of Mellanby (1935, 1936), Johannsen and Butt (1941) and Beament (1946*a* and 1949), all of whom studied eggs that are fertilised in the oviduct.

After fertilisation the egg is surrounded by the fertilisation membrane, which in *Rhodnius* is thinnest under the operculum. Inside the fertilisation membrane, and clearly recognisable as surrounding the oocyte until after the formation of the endochorion, is the vitelline membrane.

Outside the vitelline membrane is the sub-chorial membrane; it consists of the primary wax layer, the fertilisation membrane and the epembryonic membrane.

The serosa is formed from the extra embryonic blastoderm; this and the amnion are absorbed into the embryo via the dorsal organ.

The third membrane, secreted by the pleuropodia, is formed outside the serosa and amnion. In *Rhodnius* it encloses some of the extra embryonic yolk that is later absorbed; it is sac-like in form and does not enclose each appendage separately.

The embryonic cuticle develops over the whole surface of the embryo and envelops each appendage separately; it is shed immediately after eclosion. Strictly it should be considered as the cuticle (and subsequently, exuvium) of the first larval instar, thus giving a total of six larval instars in most Heteroptera. An exactly analagous situation is known in the Odonata, where Tillyard (1917) refers to the cuticle as the pronymphal sheath and states that the pronymph really represents the first larval instar. From the point of view of this study the third membrane and embryonic cuticle are most important.

Johnson (1934*b*) first described a subopercular yolk plug in *Notostira erratica* L. It appears early in the development of the egg and remains until hatching as a plug at the anterior end of the embryo and just below the operculum (fig. 5D). Usinger (1945) has observed it in another Mirid, whilst the author has found that one develops in *Capsus ater* L., *Leptopterna dolabrata* (fig. 5D) and in the Nabid, *Nabis limbatus* (fig. 5H). In some Mirids the walls of the yolk plug are dark and so fertile eggs can be distinguished soon after laying by the development of a dark band below the operculum.

Towards the end of development the red pigmented eyes and the outlines of the appendages become visible through the chorion. The successive changes in the external appearance of the egg of *Oechalia* have been described by Usinger (1941); in this species, as in all Pentatomomorpha, the median egg-burster becomes visible after the eyes in a median position between them.

Hatching.

At hatching air is taken into the gut; the body fluids are pumped into the head which swells. The process has been described in detail by Sikes and Wigglesworth (1931) for *Cimex*, Johnson (1934*b*) for *Notostira*, Johnson (1936) for *Stephanitis*, Pendergrast (1952) for *Rhopalimorpha* and by many others.

In the Cimicomorpha the swelling of the embryonic head forces the operculum upwards, breaking it at the sealing bar and so allows the larva to escape from the chorion (figs. 5D and E). Sikes and Wigglesworth (1931) and Galliard (1934*a*, *b*) have described in *Cimex lectularius* (Cimicidae) and *Triatoma vitticeps* Stål (Reduviidae) respectively, two rows of teeth on the anterior head region of the embryonic cuticle running from near the eyes to the outer margin of the labrum. Similar rows of teeth have been found by the author in two species of *Rhinocoris* (Reduviidae) (fig. 5C), in *Empicoris vagabundus* L. (Reduviidae) (Southwood 1955*a*) and in *Nabis limbatus* (Nabidae) (fig. 5H), where they take the form of crenulate toothed ridges.

Johnson (1934) described two sclerotised bands on the embryonic cuticle of *Notostira erratica* (Miridae). These are present in the mid-line just ventral to the eyes and from their junction a wavy sclerotised band runs backwards over the head ending just dorsal to the eyes. The author has found a similar structure on the embryonic cuticle of two other Mirids, *Capsus ater* and *Leptopterna dolabrata* (fig. 5F), but in the latter it is entirely straight.

Sikes and Wigglesworth (1931) suggested that the rows of teeth in *Rhodnius* tear the third egg membrane during hatching and called them the hatching spines. It seems very probable that this is their major function, but the ridges of the Miridae are more likely to serve as strengtheners to the head, which has to force up the operculum and yolk plug, and burst the anterior wall of the latter. The median region of this wall has a characteristic shape and was called by Johnson (1934*b*) the stenopyle. As the dilated head of the embryo is forced into the yolk plug, a split appears round the stenopyle and it is through this that the embryo emerges.

In the Pentatomomorpha, where the true operculum with the weak line in the sealing bar is absent, a median sclerotised area of the vertex of the embryonic cuticle forms the "egg-burster" ("ruptor-ovi", "eisprenger"). It was first figured by Moses Harris in the "Aurelian" (1766), who, however, misidentified the egg as that of a Coccinellid. This egg-burster varies in shape, but is usually T or Y shaped; a central tooth is a frequent feature and this no doubt serves to break the chorion (fig. 5A). It is noteworthy that those groups with the thickest chorions (e.g. Pentatominae, Coreidae) have much more strongly sclerotised egg-bursters than those with thinner chorions (e.g. Lygaeidae, Cydnidae).

The author has found hatching spines, similar to those of the Cimicomorpha, in *Dalpada oculata* (fig. 5B) and it is probable that they occur more or less throughout the terrestrial Heteroptera.

Where a pseudoperculum is present this is forced off at eclosion. Generally however, the chorion is split irregularly (figs. 7G and 8A) (Andre, 1934; Makhotin, 1947). In the Acanthosomatidae the egg shell splits longitudinally (Myers, 1926; Pendergrast, 1952) and in the Enicocephalidae (Myers, 1926; Carayon, 1950*b*) an angular area of the anterior of the egg is forced off.

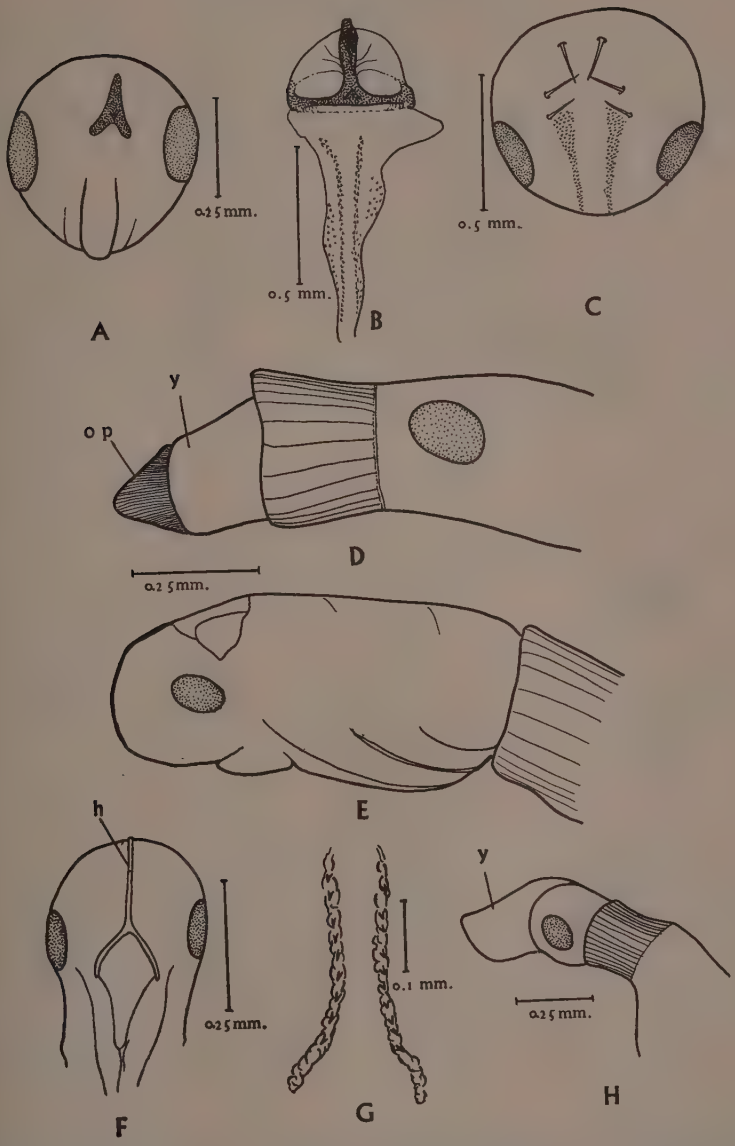


FIG. 5.—(A) *Sehirus bicolor* L., head of embryo with egg-burster. (B) *Dalpada occulata* F., egg-burster and hatching spines. (C) *Rhinocoris*, head of embryo with hatching spines. (D) and (E) *Leptopterna dolabrata* L., embryo hatching, operculum and sub-operculum yolk plug in D. (F) Ditto, anterior view of head of embryo showing hatching ridges. (G) *Nabis limbatus* Dahl., hatching spines and ridges. (H) Ditto, hatching showing sub-opercular yolk plug on anterior of head. *h*, hatching ridge; *op*, operculum; *y* sub-opercular yolk plug.

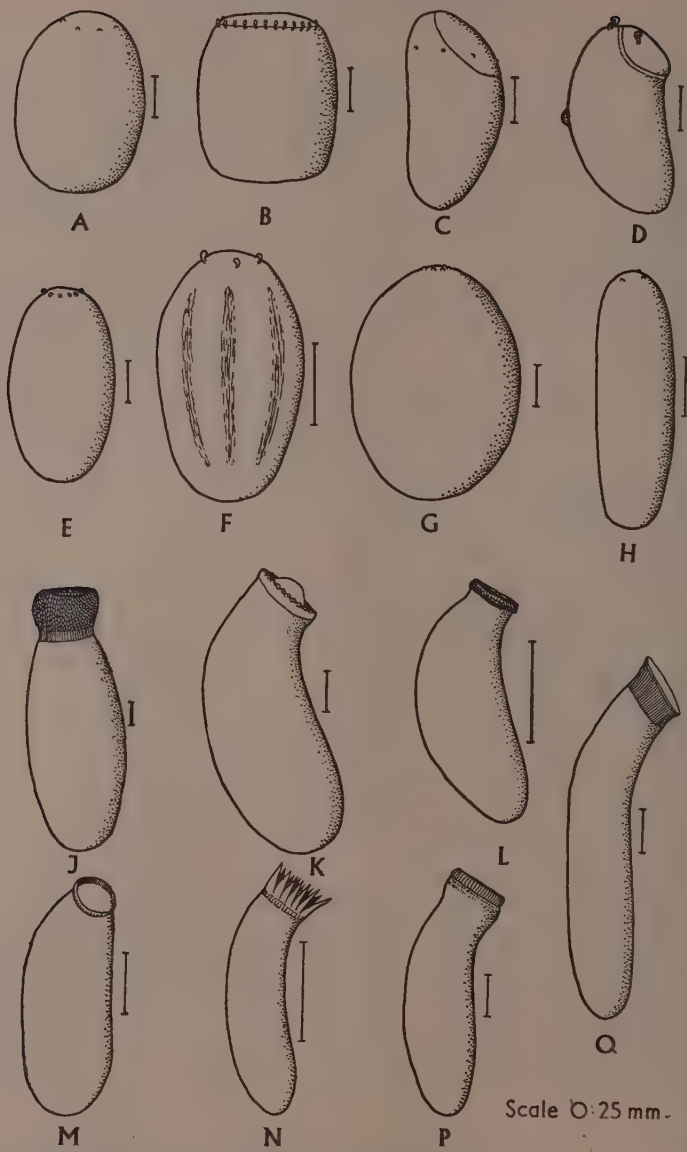


FIG. 6.—Egg forms of the terrestrial Heteroptera; (A–H). Pentatomomorpha. (A) *Sehirus bicolor* L. (Cydnidae). (B) *Stollia fabricii* Kirk. (Pentatomidae). (C) *Cletus trigonus* Thunb. (Coreidae). (D) *Chlorosoma schillingii* Schu. (Rhopalidae). (E) *Oncopeltus fasciatus* Dallas (Lygaeidae). (F) *Berytinus crassipes* H.-S. (Neididae). (G) *Dysdercus fasciatus* Signoret (Pyrrhocoridae). (H) *Aneurus laevis* Fab. (Dysodiidae). (J–Q.) Cimicomorpha.—(J) *Rhinocorus* sp. (Reduviidae). (K) *Coranus subapterus* De Geer (Reduviidae). (L) *Tingis ampliata* H.-S. (Tingidae). (M) *Cimex pipistrelli* Jenyns (Cimicidae). (N) *Loricula elegantula* Barensp. (Microphysidae). (P) *Capsus ater* L. (Miridae). (Q) *Nabis limbatus* Dahl. (Nabidae).

After emerging from the chorion, often only partially, the larva is still enclosed in the embryonic cuticle. This soon splits and is usually left attached to the empty chorion, frequently connecting the operculum to the latter. Falkenstein (1931), Risbec (1950) and others have shown that this cuticle is attached to the inside of the chorion in two or three places.

A SYSTEMATIC CONSIDERATION OF THE EGGS OF THE FAMILIES OF THE GEOCORISAE.

The information available, together with the findings of the present author on the structure of the eggs of the various families of the terrestrial Heteroptera, is given below. For certain small families no information could be found; these are: Aphylidae, Hyocephalidae, Thaumastocoridae, Joppeicidae, Leptopodidae, Aepophilidae and Leotichidae.

Pentatomomorpha.

Eggs with micropylar processes, these consisting of a central micropylar canal (for sperm passage) surrounded by the porous airsponge (for gaseous exchange); operculum absent, pseudoperculum sometimes present; median egg-burster, a single structure, present on the vertex region of the embryonic cuticle.

Pentatomoidea.

A classification of some of the families (mostly treated as subfamilies) on the structure of the egg-burster is attempted by Schumacher (1917); the variation of this structure within the superfamily is also dealt with by Miller (1934). More recently Leston (1955) has shown the relationship between egg structure and classification in this group.

Urostylidae (= *Urolabidae*).

According to Yamada (1914, 1915) the eggs are laid in two rows in crevices of the bark of oak trees. They overwinter as eggs which are completely covered with a dark yellow-green " mucus ", except for the apices of their long micropylar processes. There are usually three of these, but there is sometimes a fourth which is shorter.

The little information available supports the status of Urolabidae as an isolated family within Pentatomoidea.

Descriptions.—Miller, 1953*b*; Yamada, 1914, 1915.

Phloeidae.

Leston (1953*b*) has summarised the literature on the eggs of this family and it appears that they lack a pseudoperculum, micropylar processes and egg-burster; however, the absence of all these structures seems most unlikely.

Descriptions.—Brien, 1930; Magalhaes, 1909.

Cydnidae.

In two species of *Sehirus* Boselli (1932*a*), Southwood and Hine (1950) and Stokes (1950) have described how the female shows some degree of maternal

solicitude for eggs which are laid in the ground. Boselli mentions an egg-burster.

A re-examination of the eggs of *Sehirus bicolor* L. has shown that there is a ring of small sessile micropylar processes (figs. 6A and 7D); from the base of these run transverse micropylar canals, irregular in course and unequal in length. It is noteworthy that the shortest canal is always almost directly opposite the longest (fig. 7B).

The chorion, which is pale and very thin (2 μ), splits irregularly at eclosion. A Y-shaped, weakly sclerotised egg-burster is present on the embryonic cuticle (fig. 5A).

Several eggs of a species of *Corimelaena*, that were laid singly and laterally attached to the bracts and pedicels of a leguminous plant, were examined. They have a ring of about ten micropylar processes (fig. 7E); these, unlike those of *Sehirus bicolor*, have a distinct stalk region (fig. 7C). The chorion is pale and very thin (2μ); the transverse canals are clearly visible at the base of each process. All but one of the eggs had hatched, but from this single embryo it would appear that the egg-burster consists of little more than a median tooth (fig. 7A). At hatching the chorion splits irregularly.

Ayyar (1930) gives a very brief description of the eggs of *Stibaropus tabulatus* Schiödte. They are laid singly in the soil at a depth of 3–5 inches, near the roots of the host plant. The egg is probably somewhat similar in form to that of *Sehirus*, for it is described as "cylindrical, with smooth rounded ends". As micropylar processes were not noted, they are undoubtedly small.

Hence, from these descriptions of eggs from each of the subfamilies Sehirinae, Corimelaeinae and Cydninae, it is possible to generalise for the egg characters of the family. These seem to be a very thin simple chorion, the poles gently rounded, small micropylar processes and a weakly sclerotised egg-burster. As such they are sharply distinguished from Pentatomid eggs and show similarity to those of the Pyrrhocoridae and some Lygaeidae. This resemblance is not merely a matter of a similar oviposition site (i.e. in the soil), for those of *Corimelaena* were laid on a plant. The small micropylar processes resemble those of the Scutellerinae, Tesseratomidae and Acanthosomidae, whilst the eggs of the latter family also have a very thin chorion. The egg structure, therefore, supports the view that the Cydnidae are a separate and somewhat ancient family, closer to the Tessaratomidae than to the Pentatomidae.

Descriptions.—Ayyar, 1930; Boselli, 1932*a*; Leston and Southwood, 1954; Paul, 1953; Southwood and Hine, 1950; Stokes, 1950.

Tessaratomidae.

Tessaratomid eggs are laid in clusters and most commonly on the leaves of their host plant; they are barrel-shaped. Although frequently overlooked by authors, a ring of small micropylar processes probably occur in all species. Leston (1955) has found in *Piezosternum calidum* (Fab.) that, although these processes are small, they have a distinct stem region (cf. Scutellerinae). Sharp (1889, 1892) and others have figured a pseudoperculum, but Falkenstein (1931) has shown in *Tesseratoma papillosa* Drur. that its margins do not correspond with the fracture at eclosion. The chorion frequently bears small spines. Miller (1931) found that the egg of *Eusthenes* had an equatorial band, but the nature of this is not apparent. The egg-burster is figured by Miller (1934)

(fig. 12F) for several species; it is almost H-shaped and this may be characteristic for the family.

Such evidence as is available on Tesseratomid eggs would indicate that they are closer to the Pentatomidae than are the Cydnidae or Brachyplatidae. Their eggs most closely resemble those of the Scutellerinae, especially in the lack of

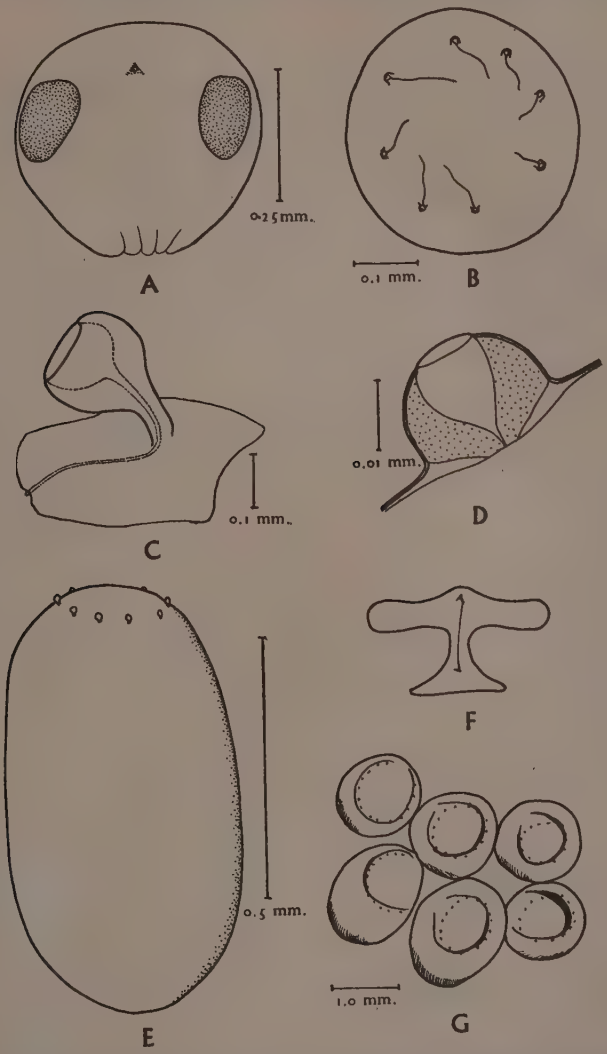


FIG. 7.—(A) *Corimelaena* sp., head of embryo with small egg-burster. (B) *Sehirus bicolor* L., anterior pole of egg showing micropylar processes and transverse canals. (C) *Corimelaena*, micropylar process. (D) *Sehirus bicolor* L., micropylar process. (E) *Corimelaena*, egg. (F) *Pycanum* F., egg-burster (after Miller, 1934). (G) *Dalpada occulata* F., egg cluster after eclosion.

a pseudoperculum and hence the irregular circular fracture on eclosion (see fig. 8A). They seem to differ from those of this subfamily in having stalked micropylar processes, though they are small in both groups.

Descriptions.—Falkenstein, 1931 ; Girault, 1924 ; Hely, 1938 ; Kershaw and Muir, 1907 ; Leston, 1955 ; Miller, 1931, 1934 ; Sharp, 1889, 1892 ; Sonan, 1935 ; Summerville, 1935.

Pentatomidae.

The eggs of this family have been described by more authors and for more species than those of any other family of Heteroptera and the list at the end of this section is by no means exhaustive. They are characteristically barrel-shaped and are laid in batches, usually upon the leaves of the host plant. The egg of *Birketsmithia* is, however, probably inserted into the heads of Composites (Leston, 1954*b*).

Makhotin (1947) and Vodjdani (1954) describe the egg of *Eurygaster integriceps;* Puton and Risbec (1950) that of *Callidea signata* F.; they have shown that the smooth chorion splits irregularly at eclosion, as the author has found in *Chrysocoris* sp. (fig. 8A). The micropylar processes are always small, being little more than protuberances (fig. 8C), and are usually about 20–30 in number. It was noted in *Chrysocoris* that they do not form a complete single circle, but are irregular in arrangement and occasionally in a double row (fig. 8A). The Scutellerinine egg-burster is shorter than that of the other Pentatomidae and is almost triangular in shape (fig. 8B). Thus the Scutellerinae would appear from the egg structure to be a relatively primitive subfamily : this is in agreement with recent views on the group, based on the study of other structures (Leston, 1954*c*).

The eggs are laid in an upright position in all subfamilies except the Dinidorinae and the Eumenotinae ; in these two they are laid on their sides in chains. In most Dinidorinae the pseudoperculum is centrally placed on the cephalic end of the egg (Miller, 1934 ; Leston, 1955), but in *Megymenum brevicorne* F. (Miller, 1929*a*) and the Eumenotinae (Maki and Tamano, 1935) it appears that the pseudoperculum is " displaced " to the side of the egg (which is dorsal). In these subfamilies the micropylar processes are very small and Leston (1955) found " some hundreds " in *Coridius cuprifer* (Westwood), a Dinidorine whose chorion was 40 μ thick and covered with many tubercles.

The Pentatominae have, in general, fewer and longer micropylar processes than the subfamilies so far mentioned. *Dalpada oculata* F., a Halyine, has about 13 micropylar processes. The chorion of the egg is covered with spines (fig. 2D) and on eclosion the fracture does not follow the line of any definite pseudoperculum (fig. 7G). Thus this egg shows some affinities to those of the Tessaratomidae and is more primitive than the eggs of the Pentatomini (figs. 6B and 8G) and Strachiini (fig. 8F), which have longer micropylar processes (about a sixteenth to a twentieth of the total egg length) and normally a pseudoperculum.

The egg of the Amyoteinae (= Asopinae) is the most highly evolved egg type in the Pentatomidae, with a smaller number (10–30) of much longer micropylar processes and a distinct pseudoperculum (fig. 8H). These micropylar processes (fig. 8K) gradually curve backwards during the development of the egg and this has been fully investigated by Mayne and Breny (1942).

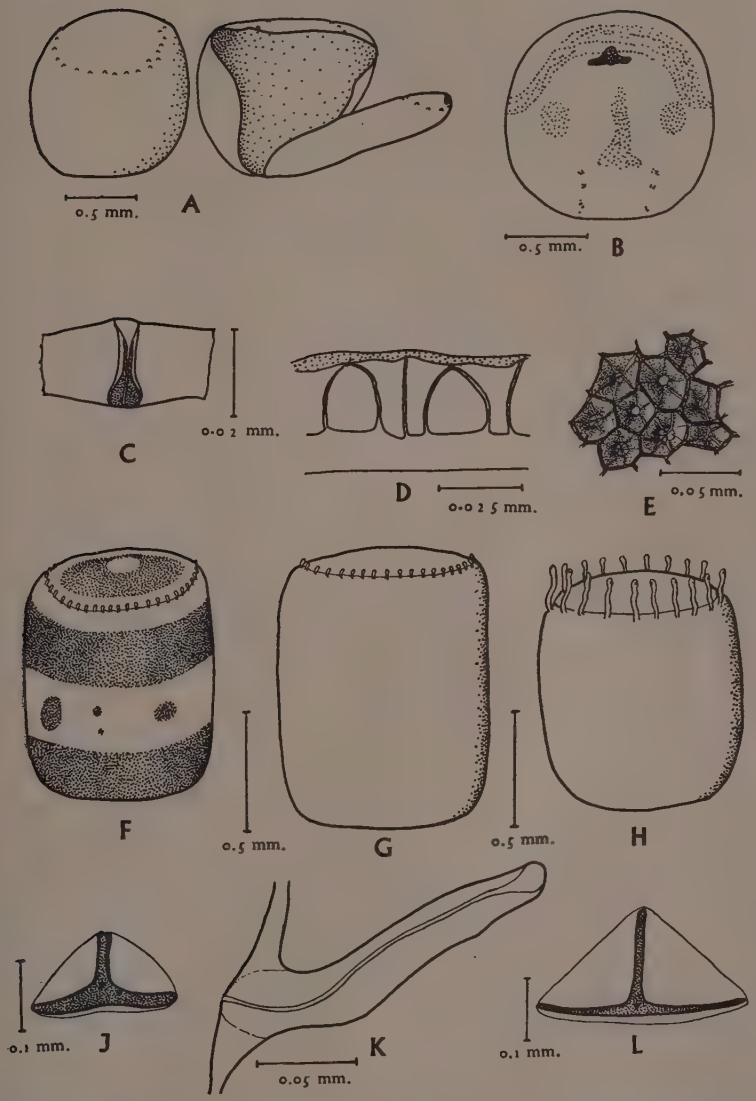


FIG. 8.—(A) *Chrysocoris*, newly laid and hatched eggs. (B) Ditto, dorsal view of egg just before hatching, showing egg-burster. (C) Ditto, L.S. micropylar process. (D) *Eurydema pulchrum* Westwood, section of chorion. (E) Ditto, surface view of chorion. (F) Ditto, eggs. (G) *Nezara viridula* L., egg. (H) *Zicrona caerulea*, egg. (J) *Stollia fabricii* Kirk., egg burster. (K) *Z. caerulea*, L.S. micropylar process. (L) Ditto, egg-burster.

The Pentatominae egg-burster, first noted by Harris (1766), is always well marked and T-shaped (fig. 8J); the egg-burster of the Amyoteinae (fig. 8L), like the structure of the pseudoperculum, is similar to that of the Pentatominae. In Dinidorinae Miller (1934) figures the egg-burster of *Megymenum* and Leston (1955) of *Coridius* (= *Aspongopus*); the latter points out the difference in the egg-burster of these two genera. These differences in both egg and egg-burster suggest that Dinidorinae as at present constituted is not homogeneous or that, at least, *Megymenum* and *Coridius* belong to different tribes. In *Dalpada oculata* (fig. 5B) the author has found two rows of teeth present on the embryonic cuticle similar to those in *Cimex* and other Cimicomorpha; it may be that careful examination will show hatching teeth to be widespread in the Pentatomomorpha.

Descriptions.—Ayyar, 1929; Balcells, 1951; Bodenheimer, 1951; Bonnemaison, 1952; Boselli, 1932*b*; Bunnett, 1947; Butler, 1923; Caffrey and Barber, 1919; China, 1926*a*; Chittenden, 1908; Couturier, 1938; Dodd, 1904; Dobsik, 1954; Dufour, 1833; Esselbough, 1946; Fabre, 1923*a*; Feytaud, 1911; Goidanich, 1943; Gross, 1901; Heymons, 1906, 1926; Ishihara, 1950; Kershaw and Kirkaldy, 1909; Kirby and Spence, 1828; Kirkaldy, 1907; Kirkland, 1897; Kobayashi, 1951, 1954; Koehler, 1948; Leston, 1955; Macgill, 1942, 1947; Maki and Tamano, 1935; Makhotin, 1947; Massee, 1943; Mayne and Breny, 1940, 1942; Michalk, 1935; Miller, 1929*a*, 1931, 1934; Miyatake and Yano, 1950; Morrill, 1910; Myers, 1926; Okamato, 1916; Olsen, 1910; Parish, 1934; Patton and Mail, 1935; Poisson, 1933; Pruthi, 1946; Rakshpal, 1950; Risbec, 1950[1]; Rosenkranz, 1939; Russell, 1952; Schouteden, 1906; Schumacher, 1910, 1917; Servadei, 1935; Strawinski, 1927; Strindberg, 1917; Summerville, 1931; Tischler, 1937; Usinger, 1941; Vodjdani, 1954; Woodward, 1949; Woodroffe and Southgate, 1952; Xambeu, 1903; Ziarkiewicz, 1953.

Brachyplatidae (= *Plataspidae* = *Coptosomidae*).

The egg batch is of a characteristic form—two rows of eggs attached to some substrate with the cephalic or micropylar ends always turned towards the outside (figs. 9C and G). There is a distinct pseudoperculum (fig. 9F) surrounded by a fringe of micropylar processes; these are extremely long in *Plataspis* and *Niamia* (Carayon, 1949*a*) and in these genera the eggs are covered by a secretion from a differentiated glandular region of the intestine, thus forming a type of ootheca. In view of the respiratory function of micropylar processes their length in these genera can perhaps be correlated with the presence of the ootheca (cf. Urostylidae).

In *Brachyplatys* (fig. 9G) and *Coptosoma* (fig. 9C) the micropylar processes are much shorter and their structure has already been described in detail (p. 169). The chorion in this family is notable for its deep follicular pits, which on laying become covered over with cement and thus form a very thick egg wall with air pockets at the base of each pit (fig. 2C). The pits are much shallower on the ventral surface of the egg where it is attached to the substrate.

[1] Mr. D. Leston has informed me that *Leptocoris griseiventris* of this paper is, in fact, a species of *Phricodus*, probably *brouini* Villiers. The egg is certainly Pentatomoid and not of the Coreoid type.

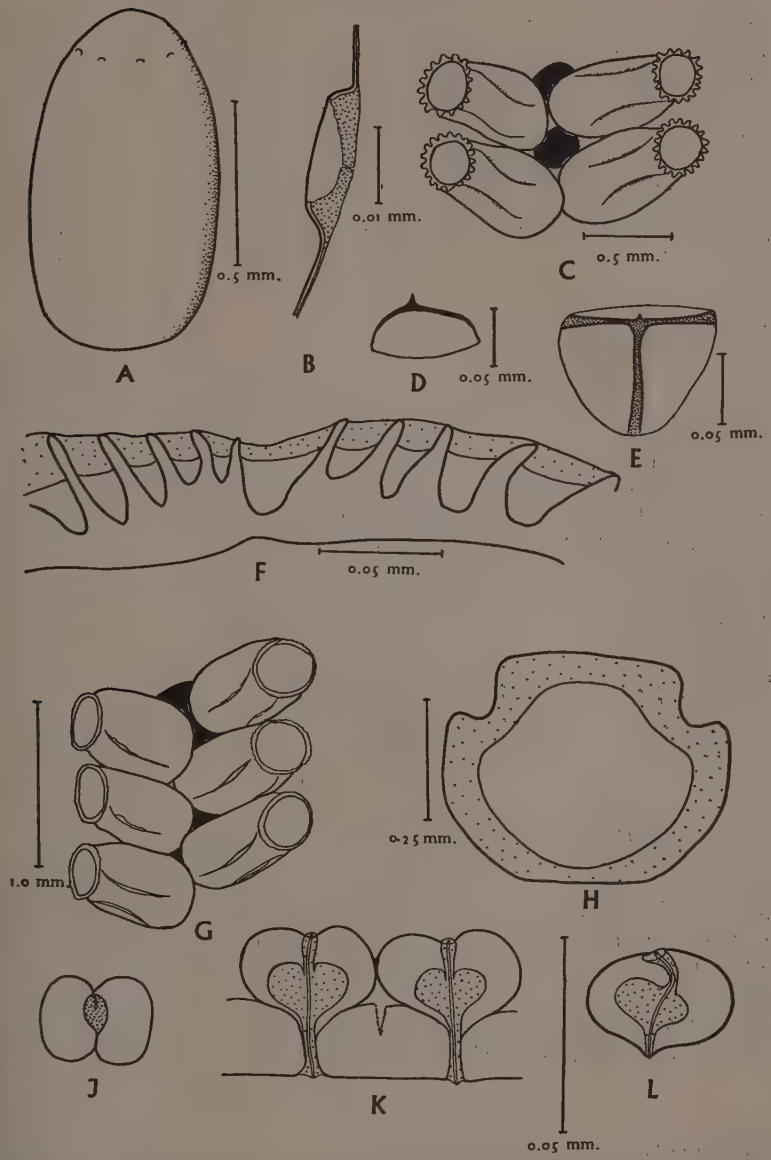


FIG. 9.—(A) *Elasmucha grisea* L., ovarian egg. (B) Ditto, L.S. micropylar process. (C) *Coptosoma cribarium* F., dorsal view of egg cluster showing symbiont pellets. (D) Ditto, lateral view of egg-burster. (E) *Brachyplatys* sp., dorsal view of egg-burster. (F) *C. cribarium*, L.S. margin of pseudoperculum. (G) *Brachyplatys*, dorsal view of egg cluster. (H) *C. cribarium*, T.S. egg. (J)–(L) *Brachyplatys*, micropylar processes, various views (J from above).

A ridge and a groove run down each side of the dorsal surface. These are due to the form of the chorion (fig. 9H) and are not superficial deposits (as in Emesinae, p. 199). As has been noted by Carayon (1952), pellets containing symbionts are deposited between the bases of the eggs (figs. 9C and G).

The egg-burster, as noted by Miller (1934), is thin and T-shaped but with a long pointed tooth (figs. 9D and E).

The structure suggests that the Brachyplatidae are a highly specialised family, close to the Pentatomidae.

Descriptions.—Carayon, 1949*a*, 1952; Kershaw, 1910; Michalk, 1935; Miller, 1934; Poisson, 1933; Schneider, 1940; Subrumanyam, 1925; Wall, 1931.

Acanthosomidae.

Acanthosomid eggs are somewhat narrowed at the cephalic pole. This is also marked by a ring of small micropylar processes (fig. 9A) that are often overlooked by other authors. There is no pseudoperculum and at hatching the chorion splits longitudinally in a characteristic fashion. Though Schumacher (1917) says that an egg-burster occurs in *Elasmucha grisea* L., this structure has not been described by other authors (including Pendergrast, 1952, who observed the hatching process carefully) and Strawinski (1951) states that, in view of Schumacher's observation, he looked for it in *E. ferrugata* F., but was unable to find it. As the chorion is thin, the egg-burster, if present, would be weakly sclerotised as in the Cydnidae (and so difficult to observe); it seems probable that this is the case. In ovarian eggs of *E. grisea* L. the chorion was found to be about 4 μ thick and the micropylar processes flat (only 50 μ high) and truncate (fig. 9B). This form of micropylar process is quite distinct from that of the typical Pentatomid and within the superfamily closest to that of the Sehirinae. The egg form shows some affinity to that of the Aradoidea and, although too much importance should not be attached to this, it is evident that the egg structure would indicate that the Acanthosomatidae is an ancient and primitive family. This supports the views of Dupuis (1948) and partially those of Leston (1953*c*), who, however, was of the opinion that they are not primitive. It would seem that this divergence of opinion has arisen because the group is ancient and should exhibit certain primitive characters, whilst its present day survival would be due to the evolution of some specialisations.

Maternal solicitude, the female remaining above the eggs until or some time after they hatch, is well known to occur in at least four *Elasmucha* (= *Meadorus*) species.

Descriptions.—Frost and Haber, 1944; Kobayashi, 1954; Macgill, 1942; Myers, 1926; Pendergrast, 1952; Strawinski, 1951.

Coreoidea.

Poisson (1951) and many earlier authors have only recognised two families, Coreidae and Hyocephalidae, within this superfamily. Unfortunately the eggs of the latter are unknown. The eggs of the Coreidae *sensu* Poisson support Reuter's (1912) view that the subfamilies Alydinae and Rhopalinae should be raised to family status. This scheme has been accepted by Blatchley (1926), Stichel (1925–38) and Dupuis (1953) amongst others, and is adopted here.

Coreidae.

The micropylar processes of the Coreidae are very small and have been overlooked by many authors; normally they form a curved row running across the pseudoperculum, as in *Physomerus grossipes* F. (fig. 10c). They vary in number: the author found 14–16 in the last species, 6–7 in *Cletus trigonus* Thunb. (figs. 10a and b) and 44–48 in *Anoplocnemus phasiana* F. (fig. 10d), all of which have been previously described without any mention of micropylar processes. Chittenden (1902) states that there are 4–6 micropylar processes in *Leptoglossus oppositus* (Say) and Heidemann (1911) found 16–18 in *L. fulvicornis* (Westw.) (= *magnoliae* Heid.), 15–18 in *Anasa tristis* (de Geer), 22 in *Euthoetha galeator* F. and "at least 40" in *Acanthocephala* (= *Metapodius*) *femorata* (F.). According to Annandale (1905) and Jordan (1933), in *Dalader* and *Spathocera* respectively, the micropylar processes, instead of running across the pseudoperculum, surround it in a ring. These observations require confirmation.

In all Coreidae the chorion is light or dark brown and generally rugose. Often, however, as pointed out by Miller (1929*b*) for *Physomerus grossipes* F., the pseudoperculum is smoother; an hexagonal sculpturation is visible in many species. The egg-burster is curved in shape (figs. 10f and l) and has been previously described by Heymons (1926) and Miller (1934, 1936).

Most Coreidae lay their eggs singly or in batches (Miller, 1934, and others), but in *Leptoglossus* (Chittenden, 1902; Heidemann, 1911) and *Anoplocnemus phasiana* (fig. 10h) (Fletcher, 1919; Miller, 1934) they are placed end to end in chains. In these species part of the dorsal surface of the chorion becomes modified to form the pseudoperculum (figs. 10c).

In *Cletus trigonus* and *A. phasiana* it has been seen that the young larva is orientated in the egg so that its venter and appendages lie towards the dorsal surface of the chorion (fig. 10a). Thus the Coreid egg is usually attached to the substrate by its side, rather than by the posterior pole as in most Pentatomoids.

Apart from Annandale's (1905) and Jordan's (1933) descriptions and the specialised chain-laid eggs of *Anoplocnemus* (fig. 10h) and *Leptoglossus*, all Coreid eggs are of similar shape and structure to those of *Cletus* (figs. 6c and 10b) and *Physomerus* (figs. 10c). They differ markedly from those of the Alydidae and Rhopalidae.

Descriptions.—Annandale, 1905; Boselli, 1932*b*; Chittenden, 1902; van Dinther, 1953; Fletcher, 1919; Heidemann, 1911; Heymons, 1926; Hoffmann, 1927, 1933, 1934*b*; Ishihara, 1950; Jordan, 1933; Kirkaldy, 1907; Merti, 1940; Miller, 1929*b*, 1931, 1934, 1936; Morrill, 1910; Peneau, 1921; Poisson, 1933; Risbec, 1950; Slater, 1943; Thomas, 1955; van der Vecht, 1933.

Rhopalidae.

The eggs of the Rhopalidae are very characteristic, with two large S-shaped micropylar processes, one of which is situated on the pseudoperculum and one below it (figs. 6d and 10n). A short stalk on the ventral surface of the egg, which, as in the Coreidae, corresponds to the ultimate dorsum of the larva, attaches it to the substratum. Sections (fig. 10p) have shown that this stalk

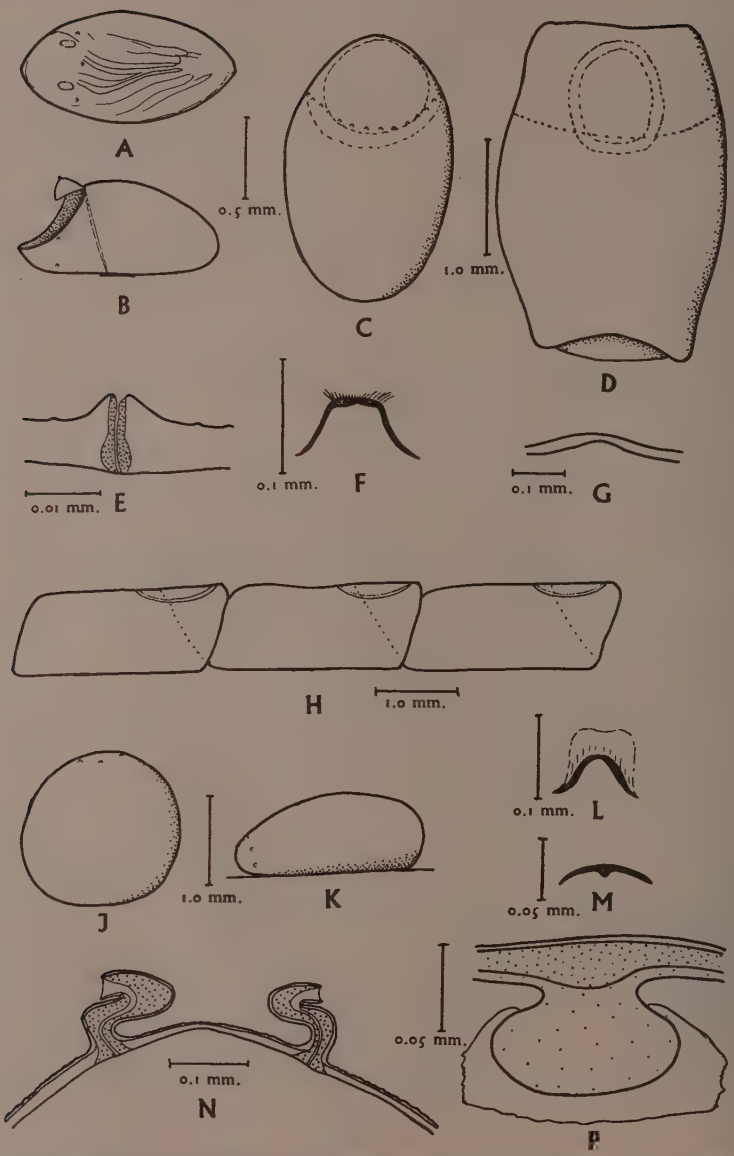


FIG. 10.—Eggs of the Coreoidea. (A) *Cletus trigonus* Thunb., dorsal view of egg just prior to hatching. (B) Ditto, after hatching, lateral view. (C) *Physomerus grossipes* F., egg, dorsal view. (D) *Anoplocnemus phasiana* F., ditto. (E) *C. trigonus*, L.S. micropylar process. (F) Ditto, egg-burster. (G) *A. phasiana*, section through margin of pseudoperculum. (H) Ditto, lateral view of egg chain. (J) *Riptortus tenuicornis* Dallas, egg, dorsal view. (K) Ditto, lateral view. (L) *A. phasiana*, egg-burster. (M) *R. tenuicornis*, ditto. (N) *Myrmus miriformis* Fallén, L.S. anterior pole of egg. (P) Ditto, L.S. basal attachment.

consists of chorion, almost entirely exochorion. Contrary to the findings of Poisson (1933), both micropylar processes possess canals (figs. 3B and 10N), and these have already been described (p. 171). The chorion is usually rugose (fig. 2E) and brown in colour. Woodward (1952) has shown how the egg of *Myrmus miriformis* Fallén, which passes the winter in a state of diapause, is completely independent of external water for its development.

The egg form of the Rhopalidae is similar to that of the Coreidae, but the presence of only two micropylar processes and the attachment stalk would seem to be a more specialised state.

Descriptions.—Butler, 1912; Ekblom, 1928; Kirkaldy, 1907; Michalk, 1935; Miller, 1931; Poisson, 1933; Readio, 1928; Risbec, 1950, 1951[2]; Stroyan, 1954; Thomas, 1955; Woodward, 1952; Xambeu, 1903; Zwaluwenberg, 1944.

Alydidae.

The eggs of this family differ sharply from those of the other Coreoidea in the absence of a pseudoperculum. They are "cauldron shaped" (figs. 10J and K), with a ring of very small micropylar processes and are deposited singly or in small groups. Empty eggs of *Riptortus tenuicornis* Dallas showed that on hatching the chorion splits longitudinally and curls up. The embryonic cuticle remains attached and this possesses a crescent shaped egg-burster (fig. 10M), similar to that of the Coreidae and found for other Alydidae by Miller (1934).

The more radially symmetrical egg and the absence of a pseudoperculum would suggest that the Alydidae are more primitive than other Coreoidea. The ovarian eggs of *Dicranocephalus agilus* Scop., described by Butler (1926), would seem to show that the Dicranocephalinae are closer to the Lygaeidae than to the Alydidae.

Descriptions.—Butler, 1923; Ishihara, 1950; Kershaw and Kirkaldy, 1908; Kirkaldy, 1907; Lefroy, 1908a; Miller, 1934.

Lygaeoidea

Neididae (= *Berytidae*).

Most Neidid eggs resemble those of *Berytinus crassipes* H.-S. (fig. 6F) with the chorion light brown and sulcate, but Massee (1949) found that it is smooth in *Metatropis rufescens* H.-S. A group of four (*Metatropis*) or six (*Berytinus*) micropylar processes with transverse canals (fig. 11C) occur on the cephalic pole. There is no pseudoperculum and at eclosion the egg-shell splits longitudinally. Readio (1923) figures the empty shell of *Jalysus spinosus* (Say) with the attached embryonic cuticle and it appears that a triangular egg-burster is present. The eggs of *Berytinus* (Butler, 1913, 1914) are laid flat on the host plant, whilst in *Metatropis rufescens* they are attached at right angles by the posterior pole. Readio (1923) has pointed out that in *Jalysus*, though the egg is parallel to the surface, it is only attached at the posterior pole, so these two methods of oviposition are not as different as might appear.

The light brown chorion and form of the Neididae egg shows some similarity

[2] *Liorhypnus hyalinus* of this paper is undoubtedly a misprint for *Liorhyssus hyalinus* F., which in both papers is misplaced by Risbec in the Lygaeidae.

to that in the Orsillini (Lygaeidae), but the micropylar processes (fig. 11c) are more strongly bent.

Descriptions.—Butler, 1913, 1914, 1923; Massee, 1949; Michalk, 1935; Poisson, 1933; Readio, 1923; Risbec, 1950.

Lygaeidae (= *Myodochidae*).

The egg of *Oncopeltus fasciatus* Dallas (fig. 6E), which has already been described in detail (p. 169), is a representative Lygaeid egg with a ring of micropylar processes and a thin pale chorion without a pseudoperculum. As Andre (1934) has shown, the chorion is split irregularly at ecdysis.

The eggs of some species, e.g. *Nysius lineatus* Costa (Michalk, 1935), are attached laterally to the underside of leaves, but most species lay in semi-exposed positions, such as between the florets of composite flowers, e.g. *Nysius coenosulus* Stål (Usinger, 1942), or at the base of plants or among moss, e.g. *Drymus sylvaticus* (L.).

The only description of an egg-burster is that of Servadei (1951), who found one present in *Heterogaster urticae* (Fab.). However, if the embryonic cuticle is removed from the embryo of *Oncopeltus fasciatus* just before hatching, a raised and Y-shaped egg-burster is visible (fig. 11F). As these Lygaeid egg-bursters are weakly sclerotised, it is probable that an egg-burster is present in many species, where it has previously been overlooked.

In most species the chorion is smooth, with the hexagonal sculpturation more or less visible, but in *Beosus maritimus* (Scop.) (fig. 11E) and *Scolopostethus decoratus* (Hahn) (fig. 11D) small truncate processes cover the whole of the chorion. Usinger (1942) describes the egg of *Oceanides nubicola* (Kirkaldy), an Orsilline, as being " piceoferrugineous " in colour.

The 11–14 micropylar processes of *Oncopeltus fasciatus* (Lygaeinae, Lygaeini) are comparatively large and clavate, with a distinct stem (fig. 3A), and are situaated in a wide circle. In the Orsillini (Lygaeinae) there are only 3–6 micropylar processes; they are papilliform in *Nysius* (Jordan, 1933; Michalk, 1935; Usinger, 1942), but clavate, though very small, in *Ortholomus punctipennis* H.-S. (Jordan, 1933). In the Aphaninae (= Rhyparochrominae) there are small numbers (3–7) of truncate (*Peritrechus sylvestris* (F.) (fig. 11H) or papilliform (*Scolopostethus decoratus*) (fig. 11D) micropylar processes, situated on the extreme cephalic pole of the egg (figs. 11A and B). The eggs of the Blissinae are elongate, but similar to those of the Aphaninae with a small number of papilliform processes on the cephalic pole; four in *Blissus* (Webster, 1898; Decker and Andre, 1938, and others) and five in *Ischnodemus sabuleti* (Fallén) (Leston, 1951).

Neither Butler (1923) nor Servadei (1951) mention micropylar processes on the eggs of *Heterogaster urticae* (F.), which are laid in the soil and it may well be that in the Heterogastrinae they are very small. Jordan's (1935) description of the egg of *Cymus glandicolor* Hahn shows that it is of the typical Lygaeid form with a few small truncate micropylar processes. However, the egg of *Kleidocerys*—which has hitherto been included in the same subfamily, Cyminae —is very different. Both Classen (1922) and Jordan (1933) have described the egg of *Kleidocerys resedae* Panz.; their descriptions do not agree and, though it is probable that they were dealing with different species, there remain inconsistencies too great for intrageneric variation. Classen found a large number of

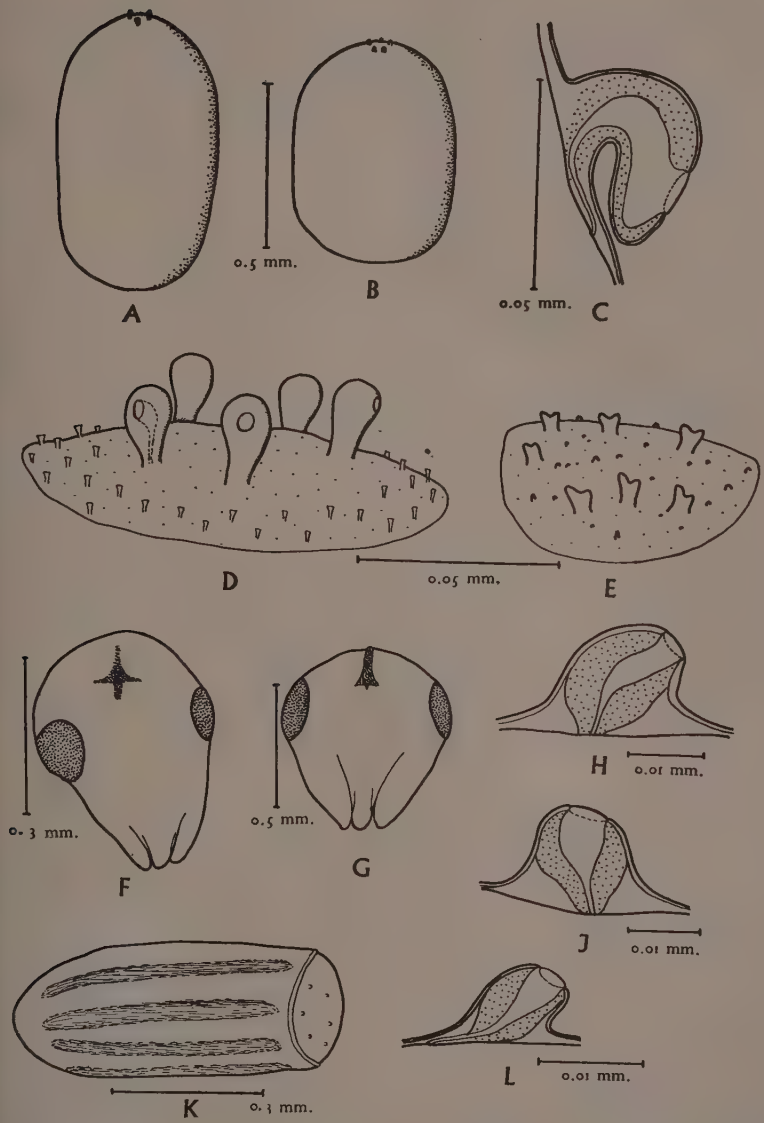


FIG. 11.—(A) *Drymus sylvaticus* F., egg. (B) *Macrodema micropterum* Curt., egg. (C) *Matatropis rufescens* H.-S., L.S. micropylar process. (D) *Scolopostethus decoratus* Hahn, dorsal pole of egg. (E) *Beosus maritimus* Scop., chorion surface. (F) *Oncopeltus fasciatus* Dallas, head of embryo with egg-burster. (G) *Dysdercus*, ditto. (H) *Peritrechus sylvestris* F., L.S. micropylar process. (J) *Dysdercus*, ditto. (K) *Piesma quadrata* Fieb., egg. (L) Ditto, L.S. micropylar process.

thin micropylar processes (" hooked spines "), whilst Jordan describes some lattice-like structures surrounding the cephalic pole. The pseudoperculum is raised in the centre and Jordan considered that the micropyle was situated in this projection. This interpretation seems unlikely to be correct. Jordan (1935) describes the egg of *Chilacis typhae* (Perris) (Artheneinae) and, like that of *Oxycarenus hyalinipennis* Costa (Oxycareninae) (Barbosa, 1951), it resembles the egg of *Cymus* or the Aphaninae in being more or less oblongate with a ring of a few short micropylar processes.

Thus the egg structure of the Lygaeidae is comparatively simple and in the Aphaninae, Artheneinae, Oxycareninae, Blissinae and *Cymus*, it resembles that of the Pyrrhocoroidea, so far as the number and structure of the micropylar processes are concerned.

The light brown eggs of the Orsillini show some similarities to those of the Neididae and it may be that this tribe deserves higher status than commonly accepted. Leston (*personal communication*) is also of the opinion that Lygaeini and Orsillini are not consubfamilial and points out that the cytology (as elucidated by Pfaler-Collander (1941)) and other data support this view.

The egg of *Kleidocerys* shows that this genus cannot be included in the same subfamily as *Cymus*. This is supported by the general morphology (Gulde, 1936) and the cytology (Pfaler-Collander, 1941) and the presence of wing stridules in *Kleidocerys*, absent from *Cymus* (Leston, *personal communication*).

Description.—Andre, 1934 ; Barbosa, 1951 ; Boselli, 1932*b* ; Butler, 1923 ; Butt, 1949 ; Classen, 1922 ; Decker and Andre, 1938 ; Ekblom, 1926 ; Heidemann, 1911 ; Hoffmann, 1934*a* ; Janes, 1935 ; Jordan, 1933, 1935 ; Kelly and Parks, 1911 ; Leston, 1951 ; Michalk, 1935 ; Miller, 1934 ; Poisson, 1933 ; Rahman and Nath, 1939 ; Risbec, 1950 ; Schneider, 1940 ; Servadei, 1951 ; Simanton and Andre, 1936 ; Slater, 1951 ; Swezey, 1945 ; Usinger, 1942 ; Webster, 1898 ; Wilson, 1929 ; Woodward, 1949 ; Zimmerman, 1948.

Colobathristidae.

The obliquely set pseudoperculum of the eggs of *Phaenacantha* species (Illingworth, 1921 ; Bolle and Stammeshaus, 1929) distinguishes them from any Lygaeid egg to which they bear many similarities in other structural features. The micropylar processes are arranged in a circle on the pseudoperculum : they are irregularly placed and mostly near the lower margin (fig. 12A). The eggs are laid in the soil, amongst trash or at the base of the host plant.

Descriptions.—Bolle and Stammeshaus, 1929 ; Illingworth, 1921.

Piesmidae.

Although a distinct pseudoperculum would appear to be present in the egg of *Piesma quadratum* Fieber, it was found that at eclosion the fracture did not always correspond with its border. Six sessile micropylar processes are normally situated on the cephalic pole (fig. 11L). The micropylar canal is comparatively stout and the transverse region is present but short. The pale brown chorion is covered with short peg-like processes and is longitudinally sulcate (fig. 11K). The eggs are attached laterally to the underside of the leaves of various Chenopodiaceae (the usual but not invariable host plants) and Wille (1929) has shown that they are subject to considerable variation in size. The author has found that

the embryonic cuticle possesses a slight thickening in the vertex region; this probably represents the egg-burster.

The Piesmid egg is obviously closely allied to that of the Lygaeidae and quite distinct from that of the Tingidae, with which family so many authors have associated the Piesmidae.

Descriptions.—Barber, 1924; Jez, 1936; Poisson, 1933; Wille, 1929.

Pyrrhocoroidea **stat. nov.**

China (1954) has recently raised the Larginae to family rank with the words: "The Larginae are now generally regarded as a distinct family more nearly related to the Lygaeidae than to the Pyrrhocoridae, which are allied to the Coreidae". Until more published evidence is available it is proposed to retain the two families within this new superfamily; as they are supposedly related to both the Coreoid and Lygaeoid stems, they cannot be placed in either superfamily. They are distinguished from the Lygaeoidea, in which they were formerly placed, by the absence of ocelli, the more elaborate venation of the membrane and other characters.

Pyrrhocoridae.

The eggs of both *Dysdercus* and *Pyrrhocoris* are characterised by their almost spherical form (fig. 6G), with a circle of small parallel-sided micropylar processes (fig. 11J) on the cephalic pole. The pale thin chorion splits irregularly at eclosion. A weakly sclerotised Y-shaped egg-burster, similar to that of *Oncopeltus*, is present in *Dysdercus* (fig. 11G), though it has not previously been noted.

Dysdercus eggs are laid in masses in sand, soil or similar material (Morrill, 1910) and are sensitive to humidity changes (Altson, 1933). *Pyrrhocoris* has similar oviposition habits (Hausmann, 1802).

Descriptions.—Barbosa, 1950; Hausmann, 1802; Köhler, 1903; Lefroy, 1908*b*; Miller, 1932; Morrill, 1910; Myers, 1927; Niklas, 1935; Singh, 1923; Vrydagh, 1942.

Largidae.

Heidemann (1911) figures and describes the egg of *Largus* (= *Euryophthalmus*) *succinctus* (Linn.). The micropylar processes appear similar to those of *Dysdercus*, but the egg is more elongate and resembles that of *Oncopeltus* (fig. 6E) in shape. The chorion is smooth and pale. Myers (1927) describes the eggs of the related *L. sellatus* Guer. as similar and, on hatching, their chorion splits longitudinally. Thus the eggs of the Largidae and Pyrrhocoridae are very similar in structure, differing only in general shape.

Descriptions.—Heidemann, 1911; Myers, 1927.

Aradoidea.

Aradidae.

The egg of *Aradus debilis* Uhler is typical of the Aradidae in being fairly elongated with a ring of about five small micropylar processes (fig. 12D). Barber

(1923) reports a distinct cap in *A. quadrilineatus* Say, but there is no sign of a pseudoperculum in *A. debilis*, neither has one been reported in any other Aradid egg and it is probable that his observation was incorrect. The chorion is transparent and thin, often showing the hexagonal sculpturation clearly. An egg-burster similar to that of *Aneurus* (fig. 12C) is figured by Jordan (1932*a*) for *Aradus cinnamomeus* Panzer. Aradid eggs are laid loosely attached laterally under bark scales or under the bark itself, generally singly, but often a number are found in the same area.

Descriptions.—Barber, 1923 ; Heidemann, 1911 ; Jordan, 1932*a* ; Krausse, 1919 ; Strawinski, 1925.

Meziridae (= *Dysodiidae*).

Eggs of *Mezira reducta* Van Duzee (fig. 12E) are oblong with three micropylar processes at the cephalic pole. The hexagonal sculpturation of the transparent and thin chorion is clearly visible ; the micropylar processes are short (fig. 12G). The eggs of the Isoderminae are unknown.

Description.—Heidemann, 1911.

Aneuridae.

Aneurid eggs are elongate with a small number of micropylar processes, usually three, at the cephalic pole, as in *Aneurus laevis* F. (fig. 12F). The chorion is thin and transparent, but the hexagonal sculpturation is not well marked. The micropylar processes are short, truncate in form, with a transverse canal (fig. 12F). The egg burster is thin (fig. 12C), and the chorion splits irregularly at eclosion. The eggs are laid singly under bark and are feebly attached to the substrate along their longitudinal axis.

The eggs of the Aneuridae are very similar to those of the Aradidae and the Meziridae, differing from those of the former in number of micropylar processes and from both families in weak hexagonal sculpturation of the chorion. Certain features of the Aradoid egg, the thin simple chorion, the absence of a pseudoperculum and the small truncate micropylar processes, are also common to the Acanthosomidae, Cydnidae and Pyrrhocoroidea. How far this is due to retention of primitive characters or to convergence consequent upon oviposition habits cannot, at present, be stated.

Descriptions.—Myers, 1921, 1926.

Termitaradidae.

The eggs of *Termitaradus trinidadensis* Morrison were examined by the author. They are subspherical in shape and the developing embryo is clearly seen through the transparent and very thin (less than 1 μ) chorion (fig. 12H). Using a phase-contrast microscope and under very high power a circle of five very small micropylar processes could be seen at the anterior pole of the egg. A very short transverse canal was found. Myers (1932) described the eggs of another species ; they were similar in shape and laid amongst the eggs of the termite host.

The eggs of this family show characters that support its association with other Aradoidea.

Description.—Myers 1932.

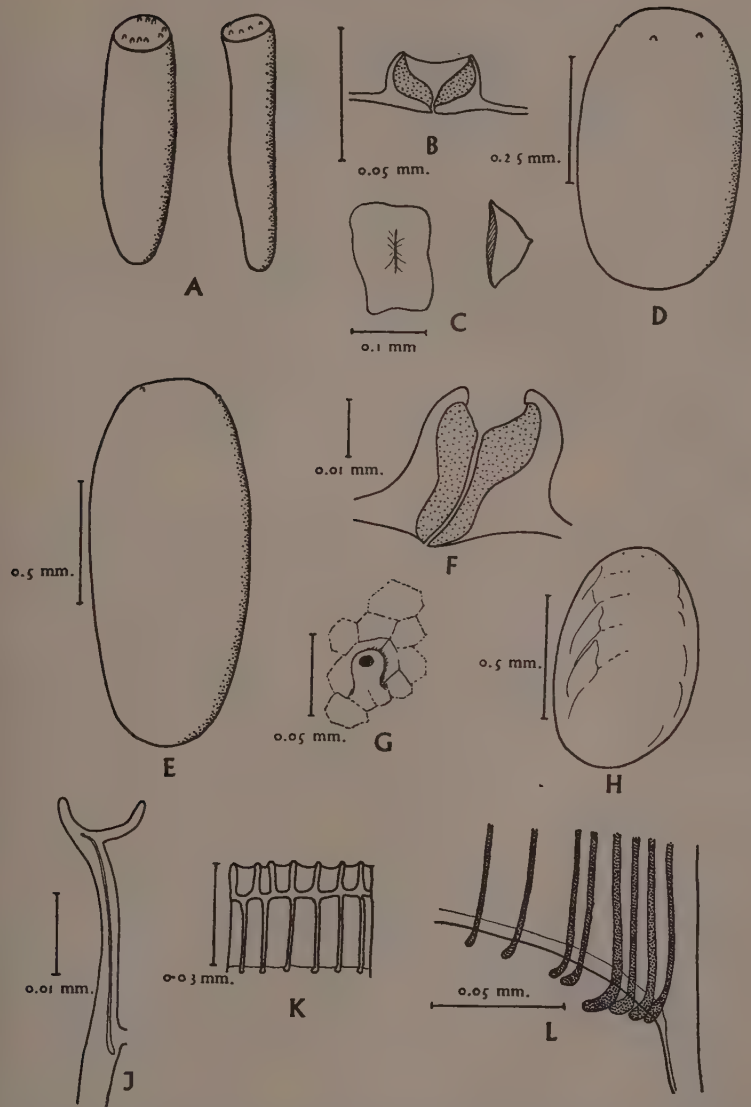


FIG. 12.—(A) *Phaenacantha australica* Kirk., eggs (after Illingworth). (B) *Aradus debilis* Uhler., L.S. micropylar process. (C) *Aneurus laevis* Fab., egg-burster, dorsal and lateral views. (D) *Aradus debilis*, egg. (E) *Mezira reducta* Van Duzee, egg. (F) *Aneurus laevis*, L.S. micropylar process. (G) *M. reducta*, dorsal view of chorion and micropylar process. (H) *Termitaradus trinidadensis* Morrison, egg with outlines of embryo visible. (J) *Xylocoris flavipes* Reut., L.S. rim of chorion. (K) Ditto, inner view. (L) *Leptopterna dolabrata* L., base of pseudomicropyles after cobalt sulphide injection.

Cimicomorpha.

Eggs with micropylar apparatus consisting of canals running in the rim of the chorion and surrounding the operculum, which is always present; the canals of two types, true micropyles (for sperm passage) and pseudomicropyles (for gaseous exchange), but one type may be absent; operculum strongly differentiated from the rest of the chorion with deep follicular pits; median egg-burster absent.

Reduvioidea.

Carayon (1950*a*) removed the Nabidae from this superfamily to the Cimicoidea; Poisson (1951) removed the Enicocephalidae to a subfamily of its own. Thus the Reduvioidea as now restricted consists only of the Reduviidae and Phymatidae. It is interesting to note that Usinger (1943), when discussing the classification of the superfamily, remarked how the eggs of *Nabis* and *Prostemma* differed from all other known Reduviid eggs. Carayon's (1950*a*) work has subsequently shown that this difference reflects a real phylogenetic incongruity in the superfamily as constituted at that time.

Reduviidae.

Reduviid eggs are in general elongate, with micropyles and pseudomicropyles, the latter joining an often large network region. The operculum is frequently thick or with a central prominence. The operculum and micropylar apparatus of *Rhinocoris* has already been described in some detail (p. 171, figs. 4A and C, 6J). This represents the most highly elaborated network region in the family, whilst in *Rhodnius prolixus* Stål, investigated in great detail by Beament (1946*a*, *b*, 1947, 1948, 1949), the network region is completely absent. Poisson (1933) recognised that there were two types of canal in the Reduviidae but he labelled what are now known to be pseudomicropyles as "tigelles de soutien de la collerette".

The eggs are never embedded in plant tissues. They are frequently attached to the substrate in either the vertical or horizontal position in compact groups (e.g. *Rhinocoris*) and the whole mass, with the exception of the rim of the chorion and the operculum, is covered with cement from the accessory glands of the female. Kershaw (1909) describes in detail the movements of the female of *Sycanus croceovittatus* Dohrn during the formation of an egg cluster. In other species, especially the Reduviinae, the eggs are laid singly with comparatively little cement, either loose amongst litter or inserted into crevices. Beament (1947) showed that in *Rhodnius prolixus*, though the true micropyles are occluded by this cement at oviposition, the pseudomicropyles remain exposed. In the Emesinae the eggs are firmly "cemented" to the substrate and generally covered with "ribs of cement".

Galliard (1934*a*, *b*) and Tilden (1949) have described the two rows of hatching spines on the head region of the embryonic cuticle of *Triatoma vitticeps* Stål and *Pselliopus spinicollis* Champion respectively. Sikes and Wigglesworth (1931), when describing similar structures in *Cimex*, record them in *Rhodnius prolixus*, whilst the author has found them in *Rhinocoris* sp. (fig. 5C) and curved spinose ridges in *Empicoris vagabundus* (L.) (Southwood, 1955*a*). Thus hatching spines are probably present throughout the Reduviidae.

At present a very large number of subfamilies (at least 23) are recognised

within the Reduviidae. It is the author's opinion that it is unlikely that all these are of the same rank and that subsequent workers may well revise the classification considerably. When this is done the characters furnished by the eggs should be considered along with those of a more orthodox nature. From the early survey of Readio (1926) and subsequent accounts, especially the monumental work of Miller (1953*a*) and that author's useful pactice of figuring ovarian eggs in taxonomic works (Miller 1954*a*, *b*, *c*, *d*), it has been possible to give the following survey of the egg forms of most Reduviid subfamilies.

Emesinae.—The very elongate, spindle-shaped eggs are distinguished by this feature alone from all other Reduviid eggs except those of *Rhaphidosoma* and related Harpactorine genera (Miller, 1953*a*). The network region is very small, but the operculum has a central prominence, short in *Empicoris* (Southwood, 1955*a*), longer in *Emesaya* (Readio, 1926) and *Mayemesa* (Wygodzinsky, 1944*b*) and extraordinarily long in *Stenolaemus* (Miller, 1953*a*), where it is surrounded by shorter filaments. The chorion is always brown or black. A characteristic of all Emesine eggs would seem to be the method of depositing the cement in ridges, either continuous or broken (as in *Empicoris huttoni* (Scott) (Myers 1926)), along the longitudinal axis of the egg. Emesine eggs are always laid singly.

Stenopodinae.—Readio (1926) figures the egg of *Oncocephalus apiculatus* Reuter. It is laid in the ground with only the operculum exposed and is subspherical with a small network region and a tuft of short filaments in the centre of the operculum. These characters are sufficient to distinguish it from all other Reduviid eggs, but it shows some similarities to the Emesinae and the Harpactorinae, although differing from both these subfamilies in having a pale chorion.

Harpactorinae.—The egg form is known in 26 genera of this large subfamily. In *Rhaphidosoma* and *Lopodytes* the very elongate eggs are placed singly or occasionally in small groups on grass stems (Miller, 1953*a*). In the other genera the eggs are usually bottled-shaped as in *Rhinocoris* (fig. 6J) or *Coranus* (fig. 6K), being widest in *Bequeartidea*. They are frequently deposited in groups on some substrate and are copiously covered with cement (Kershaw, 1909). As Miller (1953*a*) has pointed out, these groups vary in number from five to several hundred; a range almost as large as this may be found within one species. The eggs of this subfamily are characterised by the dark chorion, with the pale network region and operculum, which has a central prominence (i.e. deep follicular pits). The greatest complexity is found in *Rhinocoris* (figs. 4A and C) and *Pearius*, where the top of the long network region is joined to the centre of the operculum. An intermediate condition is found in genera such as *Hoffmanocoris* and *Paramphibolus* (Miller, 1953*a*), whilst the network region is smallest in *Coranus* (fig. 6K) and *Coronopsis* (Miller, 1953*a*). The network region and a central opercular prominence are, however, always present, though *Leptodema* (Miller, 1953*a*) would appear to be aberrant in this respect.

Apiomerinae.—Heidemann (1911), Morgan (1907) and Readio (1926) have described the eggs of two species of *Apiomerus* and they are similar in colour and shape to those of *Rhinocoris*, but, although the network region is well developed, the operculum is " rather low " and " sunken in the middle ". It is evident that the egg structure supports Usinger's (1943) view that this subfamily is close to the Harpactorinae.

Physoderinae.—This subfamily was proposed by Miller (1954*b*) for the genus

Physoderes, which had hitherto been included in the Reduviinae. Miller figures ovarian eggs which, as he remarks, closely resemble those of the Harpactorinae (especially *Coranus*) and would be quite atypical for any member of the Reduviinae.

Phonolibinae.—Miller (1952) raised this subfamily for the genera *Phonolibes* and *Lophocephala* which had previously been placed in the Tegeinae. According to Miller the latter should only include the genera *Tegea* and *Campylorhyncha*. The egg of *Phonolibes obsoletus* Horvath has been described by Miller (1953*a*); it is brown with a pale well developed network region and appears to show a strong resemblance to the egg of *Peprius pictus* Miller (Harpactorinae).

Piratinae.—The long filamentous processes from the rim of the chorion of the pale or greyish eggs of this subfamily give them a star-like appearance and distinguish them from all other Reduviid eggs. They are laid in the soil with only these processes (probably part of the network region) projecting (Readio, 1926; Miller, 1953*a*). The operculum is flat and the general form of the egg bottle-shaped.

Salyavatinae.—Miller (1953*a*) has described the eggs of *Petalochirus* and *Lisarda* spp. and they are very characteristic in form, being almost equidimensional, polyhedral in the former and spherical in the latter. In *Lisarda* the operculum has a small central prominence. The greenish or reddish eggs are scattered loosely on the ground; there appears to be little or no cement spread over them (Miller, 1953*a*).

Reduviinae (= *Acanthaspinae*).—It is almost entirely due to the work of Miller (1953*a*) that the eggs of seven genera of this subfamily are now known. They are always laid singly amongst the soil or debris. The network region is very small or absent, the operculum flat and the chorion light brown.

Triatominae.—The eggs of various species (Abalos and Wygodzinsky, 1951), and especially of *Rhodnius* (Beament 1946*a*, *b*, 1947, 1948, 1949; Tuft, 1950), are well known. The chorion is white, the operculum thin and the network region absent. The eggs are laid singly.

Ectrichodiinae.—Miller (1953*a*) has described the eggs of *Maraenaspis*, *Glymmatophora* and *Ectrichodia*. They are deposited loosely in the soil and resemble those of the Reduviinae and Triatominae in structure. This suggests that this subfamily is more closely related to the two last named than was considered by Usinger (1943).

In conclusion it has been shown that, contrary to the statements of some workers, it is possible to allot egg characters to the Reduviid subfamilies (the only aberrant genus is *Leptoderma*). The egg types of the Emesinae, Stenopodinae, Piratinae and Salyavatinae are all unique. The Harpactorinae, Apiomerinae, Physoderinae and Phonolibinae share a common egg type characterised by the presence of the network region (not fragmented) and the operculum thickened, at least in part. The eggs of the Reduviinae, Triatominae and Ectrichodiinae are similar in shape; the network region is very small or absent and the operculum thin and almost flat.

The Reduviid egg shows close similarity to that of the Phymatidae, and the egg structure confirms Carayon's (1950*a*) and Poisson's (1951) removal of Nabidae and Enicocephalidae respectively from the Reduvioidea. It can be seen how the Cimicoid egg, especially that of the Nabidae, could have evolved from an egg of the Harpactorine type by the reduction of the network region and the loss

of the true micropyles (fig. 4c). The Tingid egg also resembles the Reduvioid egg, but lacks pseudomicropyles.

Descriptions.—Abalos and Wygodzinsky, 1951 ; Beament, 1946*a*, *b*, 1947, 1948, 1949 ; Bequaert, 1912 ; Bose, 1951 ; Campos, 1923 ; China, 1926*b* ; Fabre, 1923*b*, Galliard, 1934*a*, *b* ; Girault, 1906 ; Heidemann, 1911 ; Hoffmann, 1934*c*, 1935*a* ; Iragorry, 1934 ; Kershaw, 1909 ; Kirkaldy, 1907 ; Korschelt, 1887 ; Mazza, Tobar and Jorg, 1940 ; Mellanby, 1935, 1936 ; Michalk, 1935 ; Miller, 1953*a*, 1954*a*, *b*, *c*, *d* ; Morgan, 1907 ; Myers, 1926 ; Pinto, 1925 ; Poisson, 1933 ; Readio, 1926 ; Sharp, 1892 ; Southwood, 1955*a* ; Swezey, 1905 ; Tilden, 1949 ; Tuft, 1950 ; Villiers, 1949 ; Wygodzinsky, 1944*b*.

Phymatidae.

The oval egg, with its distinct operculum, of *Macrocephalus notatus* Westwood (Wygodzinsky, 1944*a*) shows the close relationship of this family to the Reduviidae. According to Balduf (1941) the eggs of *Phymata pennsylvanica* Handlirsch laid in captivity are deposited in groups of 12–19 secured to " plane surfaces " by cement. The young larvae hatch by forcing off the operculum. Wygodzinsky contrasts the fine round puncturation of the *Macrocephalus* chorion with the hexagonal Reduviid type. It is, however, just a modification of this type and, as Abalos and Wygodzinsky (1951) have shown in the Triatominae, the chorion pattern can vary from the hexagonal to the rugose or punctate type in closely allied species.

Descriptions.—Balduf, 1941 ; Fletcher, 1905 ; Handlirsch, 1897 ; Heidemann, 1911 ; Readio, 1927 ; Wygodzinsky, 1944*a*.

Tingoidea.

This superfamily now contains only the Tingidae, as Leston, Pendergrast and Southwood (1954), following Tullgren's (1918) work and other new evidence, have removed the Piesmidae.

Tingidae.

Reuter (1912) stated that the eggs of the Tingidae were unknown. However, Comstock (1879) had described the eggs of a species of *Corythuca* and subsequently numerous accounts of the eggs of the American species were published. The first adequate description in the European literature was that of Jordan (1933) for *Galeatus maculatus* (H.-S.).

The eggs are oblong and slightly tapered towards the opercular end ; they are always inserted in plant tissue (figs. 6L and 13A). In *Acalypta parvula* Fallén (Leston, 1953*a*), where they are laid in moss, they are not always completely embedded, but presumably dessication is not as great a danger in such a habitat. Johnson (1936) describes the formation of a corky gall around the overwintering egg of *Stephanitis rhododendri* Horvath. The present author has sectioned the egg of *Tingis ampliata* H.-S. *in situ* ; there was no trace of a corky gall (Southwood and Scudder, 1956).

The chorion is generally pale with the hexagonal sculpturation clearly visible, but in some species; e.g. *Monanthia humuli* (F.) (Leston, 1954*a*), it is dark brown to black. In *Dictyonota strichnocera* Fieb. only the exposed neck region is dark (fig. 13A). The micropylar and network regions of the Tingid

egg are short but when subjected to the cobalt sulphide injection technique the canals of the last named region did not become black or grey. This may, however, have been due to experimental error. The micropylar and network region of *Stephanitis rhododendri* has already been described by Johnson (1936). The present author has confirmed Johnson's findings. Only true micropyles are present and these follow a somewhat irregular course in the micropylar region, eventually opening to the surface at the bottom of longitudinal grooves in the network region (fig. 13B). The network region itself is reflexed back, so that in contrast to the Reduviid egg, not only is the spermatic groove absent as a ring round the egg, but the micropyles open on to what would be the inner surface of the rim of the chorion. The meshes of the network region decrease in size towards the micropylar region.

Roonwal (1952) gives a detailed description of the egg of *Teleonemia scrupulosa* Stål and in this species the network region, instead of being reflexed back, is produced vertically above the egg, joining over the operculum. Both Johnson (1936) and Roonwal (1952) describe instances of true micropyles fusing before reaching the network region.

Thus the Tingid egg would appear to be unique in the Cimicomorpha in lacking pseudomicropyles and the problem of its gaseous exchange for respiration remains unsolved. The arrangement of the opercular region is of two types; (*a*) with the network region and the rim of the operculum reflexed back as in *Tingis*, *Stephanitis* and *Dictyonota*, and (*b*) with the network region produced above the operculum as in *Teleonemia*.

All the eggs known in any detail belong to the Tinginae. Butler (1923) describes the egg of *Agramma laeta* (Fallén) (Agramminae) as " yellow, cylindrical rounded at one end and obliquely truncate at the other, and there are some transverse wrinkles on one side ". The single egg observed was laid on a blade of grass. This would appear to be a fairly typical Tingid egg, except for the method of oviposition, and further observations on this point are obviously desirable.

Descriptions.—Abbot, 1935; Bailey, 1951; Butler, 1923; Comstock, 1879; Dickerson and Weiss 1916, 1917; Drake 1922*a*, *b*; Fink, 1915; Fletcher, 1916; Gomez-Menor, 1950; Hoffman, 1935*b*; Johnson, 1936; Jordan, 1933; Leston, 1953*a*, 1954*a*; Morrill, 1903; Poisson, 1933; Roonwal, 1952; Samuel, 1939; Sharga, 1953; Southwood and Scudder, 1956; Usinger, 1946; Vidal, 1939; Weiss, 1919; Weiss and Dickerson, 1918; Weiss and West, 1924.

Cimicoidea.

Carayon (1950*a*) included the Nabidae in this superfamily and recently Leston, Pendergrast and Southwood (1954) have associated the Joppeicidae (whose eggs are unknown) with it. The Polyctenidae are vivaparous and are therefore omitted from this study (Hagan, 1931).

Nabidae.

The extremely elongated eggs of *Nabis limbatus* Dahlbom (fig. 6Q) or of *N. flavomarginatus* Scholtz (figs. 13E) are typical of the family, the eggs of which are always inserted into plant tissues, principally stems. The micropylar region, containing long straight pseudomicropyles, terminates in a short network region. In *N. flavomarginatus*, where the operculum is domed, this region curves

round and partially covers it (fig. 13E). The operculum is very thick, but, unlike that of the Reduviidae, there is a large cavity between its base and the base of the follicular pits (fig. 4B). Because of this the central follicular pits may be quite shallow.

The chorion is pale and simple with the hexagonal sculpturation often visible. In *N. limbatus* it has been found that a pair of crenulate toothed ridges

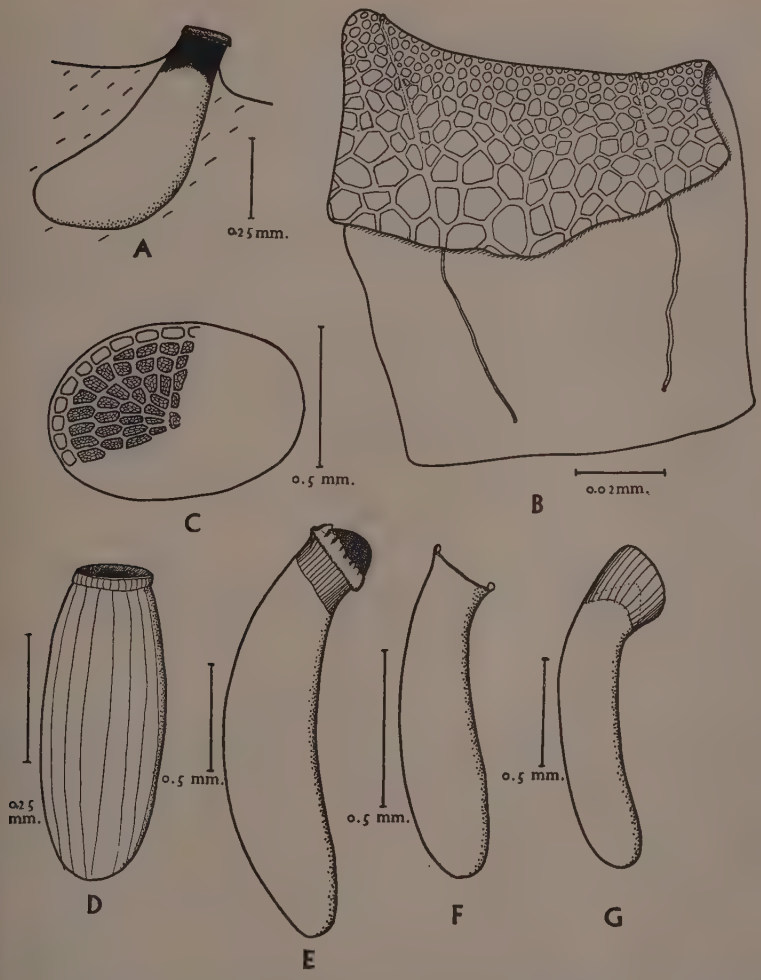


FIG. 13.—(A) *Dictyonota strichnocera* Fieb., egg in situ in gorse stem. (B) *Stephanitis rhododendri* Horv., rim of chorion with micropyles. (C) *Xylocoris flavipes* Reut., dorsal view of operculum. (D) Ditto, egg. (E) *Nabis flavomarginatus* Scholtz, egg. (F) *Dicyphus stachydis* Reut., egg. (G) *Leptopterna dolabrata* L., egg.

are present on the embryonic cuticle (fig. 5G); these are similar to those of *Empicoris* (Reduviidae). It has also been noted that a yolk plug, hitherto known only in the Miridae, is present in *N. limbatus* prior to hatching (fig. 5H).

Michalk (1935) has described the egg of *Prostemma* and it does not appear to differ markedly from that of *Nabis*.

Descriptions.—Chapman, 1906; Ekblom, 1926; Michalk, 1935; Mundinger, 1923; Poisson, 1933; Steer, 1929; Swezey, 1905.

Cimicidae.

The egg of *Cimex lectularius* L. has been described by many authors. Its chorion shows an hexagonal sculpturation and is covered with numerous fine spines that were first observed by Dufour (1833). Recently Dasgupta and Ray (1955) have claimed that the apices of these spines are inserted into the nuclei of the follicle cells and that during chorion formation globules, which stained with methyl green, passed down these spines into the chorion. Further investigations are needed before this theory of chorion formation can be accepted.

The general form of the egg of *Cimex* spp. is elongated with an almost circular operculum (fig. 6M). Wygodzinsky (1951) figures the egg of *Bertilia* and Swezey (1905) of *Oechalia*, and these are similar. Sikes and Wigglesworth (1931) described the hatching spines of *C. lectularius*; they are arranged in two rows on the face region of the embryonic cuticle.

The eggs are attached laterally to various substrata. Thus they differ from those of all the other Cimicoidea in being exposed and, as Johnson (1940, 1942) has shown, they are relatively independent of humidity changes.

It will be seen that the major characters of the Cimicid egg—the circular operculum surrounded by the simple rim of the chorion, with numerous (about 100) pseudomicropyles—show a strong resemblance of those of the Anthocoridae.

Descriptions (and accounts of fertilisation in *C. lectularius*).—Abraham, 1934; Bacot, 1921; Cragg, 1915; 1920, 1923; Dufour, 1833; Galliard, 1934*a*, *b*; Myers, 1926; Sikes and Wigglesworth, 1931; Sweżey, 1905; Wigglesworth and Beament, 1950.

Anthocoridae.

The eggs of comparatively few Anthocorids are known; they are elongate (fig. 13D), with a pale chorion often clearly showing the hexagonal pattern. The operculum is virtually circular in all species except *Elatophilus nigricornis* (Zett.) (Sands, 1954), where it is elliptical. *Acompocoris pygmaeus* (Fallén) is exceptional in having the centre of the operculum raised, for this structure is normally flat and fairly thin, with a distinct pattern (fig. 13C). Sands (1954) found this pattern to be a specific character.

The eggs of *Xylocoris flavipes* (Reuter) have been examined and have between 58 and 60 pseudomicropyles that join the circular canal at the base of the short network region (fig. 12K). This region has an inner branch that curves over the operculum (fig. 12J) and it is probably homologous with the veil that joins the top of the network region to the operculum in some Reduviids (see p. 174).

Those Anthocorids that dwell on plants always insert their eggs in the leaves

or stems of their host. The eggs of species living in stored products are laid, like those of *Cimex*, in exposed or semi-exposed situations.

The eggs of the Anthocoridae show a general similarity to those of the Cimicidae, but differ in the presence of a reduced network region. This character is also found in the Nabidae and Microphysidae. The thickened operculum of *Acompocoris* is similar to that in the Nabidae, but the elliptical-shaped operculum of *Elatophilus* is found elsewhere only in the Miridae.

Descriptions.—Collyer, 1953 ; Fulmek, 1930 ; Hall, 1951 ; Leston, 1954*a* ; Peska, 1931 ; Poisson, 1933 ; Sands, 1954 ; Swezey, 1905.

Microphysidae.

Only the eggs of *Loricula* and *Myrmedobia* have been described. These are very characteristic with tapering processes that probably correspond to the network region (fig. 6N) (Carayon, 1949*b*). The eggs of *Loricula elegantula* (Barensprung) are very large compared with the adult female, two (the maximum number found) almost filling the abdomen. These ovarian eggs have been studied and the pseudomicropyles found to be short, as in the Anthocoridae, terminating at the base of the network region. In the ovarian egg the processes of the network region touch at their tips and thus cover the operculum, but Carayon (1949*b*) found that in the laid egg they radiate out and thus their apices become widely separate. The operculum is thin and flat with a pattern, due to the follicle cells, similar to that of the Anthocoridae.

Carayon (1949*b*) found the eggs, that are grey to brown in colour, inserted amongst lichens growing on the twigs of various trees.

The Microphysid egg is, therefore, similar to the Anthocorid in some features, but differs in the fragmented network region, which is the largest in the Cimicoidea.

Descriptions.—Carayon, 1949*b* ; Thomas, 1938.

Miridae.

The eggs of Mirids are characterised by the asymmetrical operculum. This is elliptical and often concealed by the rim of the chorion, as in *Leptopterna dolabrata* (L.) (fig. 13G). Eggs of *Capsus ater* L. (fig. 6P) and *L. dolabrata* were injected with cobalt sulphide and the canals in the rim of the chorion all became filled with the black precipitate. These are pseudomicropyles which arise as small bulbous cavities in the resistant protein and are concentrated at the narrow ends of the operculum (figs. 12L) ; this is especially so in *Dicyphus stachydis* (fig. 13F). Kullenberg (1942, 1943, 1946) described and sectioned the eggs of many Mirids and, although the network region is always absent, the operculum is often very thick with the pseudomicropyles (Leuckart's canals) correspondingly lengthened, as in *Orthocephalus mutabilis* (Fallén) and *Miris striatus* (L.). This arrangement is probably analogous, but not homologous, with the large network regions of certain Reduviids. It is noteworthy that the thinnest operculum and some of the shortest pseudomicropyles are found in *Lygus pratensis* (L.), a species that overwinters as the imago and whose egg stage lasts only a few weeks, whilst in the many species where the operculum and pseudomicropyles are thick and long the egg is the overwintering stage and lasts for at least six months. The chorion is always pale, usually transparent or

yellow, but occasionally light brown. Kullenberg (1946) measured the thickness of the chorion in 17 species and it varied from 2·3 μ in *Lygus cervinus* H.-S., to 9·6 μ in *Adelphocoris seticornis* Fab.

The eggs do not appear to exhibit any subfamily characteristics in the Miridae, but it is very probable that some would be found if the number and distribution of the pseudomicropyles were further investigated. However, the eggs of closely related genera are similar and Carvalho and Southwood (1955) have found that the egg form differs in the strongly convergent genera *Cyrtohinus* (Orthotylinae) and *Tytthus* (Phylinae).

Poisson (1933) states that in *Notostira erratica* (L.) micropylar processes, clearly seen after eclosion, project from the rim of the chorion ; but, as Johnson (1934*b*) has shown, they are only jagged pieces of the rim of the chorion, containing what are now known as pseudomicropyles. They cannot, therefore, be considered as homologous with the micropylar processes of the Pentatomomorpha (as defined on p. 169).

All known Mirid eggs, with the exception of those of *Strongylocoris leucocephalus* (L.) and *Malacocoris chlorizans* (Panzer), are embedded in plant tissue with only the operculum and micropylar region, which may have a long projection as in *Helopeltis*, exposed. The chorion is always smooth or with a faint hexagonal sculpturation, except in *S. leucocephalus* and *M. chlorizans* where it is rugose (Kullenberg, 1946).

The subopercular yolk plug first described by Johnson (1934*b*, 1937) in *Notostira erratica*, has been found by Usinger (1945) and the author in other species and is probably present throughout the family.

The Mirid egg is similar to all other Cimicoid eggs in form and in lacking true micropyles. It is, however, sharply distinguished by the elliptical and often elaborate operculum and the complete absence of the network region.

Descriptions.—Abraham, 1936 ; Austin, 1931 ; Ballard, 1916, 1919 ; Bodenheimer, 1951 ; Brittain, 1917 ; Butler, 1923 ; Cagle and Jackson, 1947 ; Capco, 1941 ; Carvalho and Southwood, 1955 ; Collyer, 1952 ; 1953*a*, *b* ; Crosby, 1911 ; Dudgeon, 1894 ; Gäbler, 1937 ; Geier and Baggiolini, 1952 ; Gross, 1903 ; Harcourt, 1891 ; Johnson 1934*a*, *b*, 1937 ; Kullenberg, 1942, 1943, 1946 ; Lal, 1950 ; Lavabre, 1954 ; Leonard, 1915, 1919 ; Maki, 1918 ; Michalk, 1935 ; Poisson, 1933 ; Reinhard, 1926 ; Risbec, 1950 ; Silvestri, 1934 ; Slingerland, 1893 ; Sorenson and Cutler, 1954 ; Steer, 1929 ; Trehan and Phatak, 1946 ; Usinger, 1945 ; Wilson, 1925 ; Woodward, 1949, 1952.

Geocorisae—Incertae Sedis.

Cryptostemmatidae.

The only description and figure of a Cryptostemmatid egg is that of the ovarian egg of *Trichotanannus dundo* Wygodz., by Wygodzinsky (1953). The egg is oblong with a lid which, according to the description, has the hexagonal sculpturation less easily visible than on the rest of the chorion. From the diagram some form of chorion rim would appear to be present, but this does not seem to coincide with the margins of the " lid ". Thus the evidence is insufficient to give any indication of the systematic position of the family, as it is not clear whether a true operculum and micropylar region of the Cimicomorphan type are present.

Description.—Wygodzinsky, 1953.

Saldidae.

Jordan and Wendt (1938) described the egg of *Salda littoralis* (L.) in some detail and were unable to find any micropyles, but they state that the whole of a differentiated area at the anterior pole should be regarded as the micropylar area. The general form of the egg and the method of oviposition in plant tissue (Wiley, 1922) (as well as in mud) perhaps suggest a relationship to the Cimicomorpha. The egg-burster described by Jordan and Wendt may be homologous with the median process of the Pentatomomorpha but from its position would appear more likely to be homologous with the longitudinal ridges of the Miridae.

Descriptions.—Brindley, 1934 ; Ekblom, 1926 ; Hungerford, 1919 ; Jordan and Wendt, 1938 ; Wiley, 1922.

Enicocephalidae.

Enicocephalid eggs are subspherical in shape, without an operculum or visible micropylar region. As Carayon (1950*b*) and Myers (1926) have shown, an angular area at the anterior of the chorion splits off at eclosion. Thus the eggs of this family are quite distinct from those of any other terrestrial Heteroptera, except superficially the Termitaradidae, and show similarities to those of aquatic Heteroptera.

Summary.

The development, structure and hatching of the eggs of the terrestrial Heteroptera are shown to support the division of the Geocorisae (*sensu* Dufour, 1833) into the Pentatomomorpha and Cimicomorpha. The micropylar apparatus is of two types, the micropylar processes of the Pentatomomorpha and the pseudomicropyles and true micropyles of the Cimicomorpha. A true operculum is present only in the Cimicomorpha. The Pentatomomorphan egg normally lacks a distinct egg cap, but when one is present it is not homologous with the operculum of the Cimicomorpha and is called a pseudoperculum. Hatching spines and ridges are present in both the Pentatomomorpha and Cimicomorpha, but a median egg-burster is confined to of Pentatomomorpha.

From the present work and that of earlier authors structural characteristics of the egg are given for each family and many subfamilies. It is suggested that this evidence from egg structure should be considered, together with other evidence, when discussing the status of various groups and their phylogenetic relationships.

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